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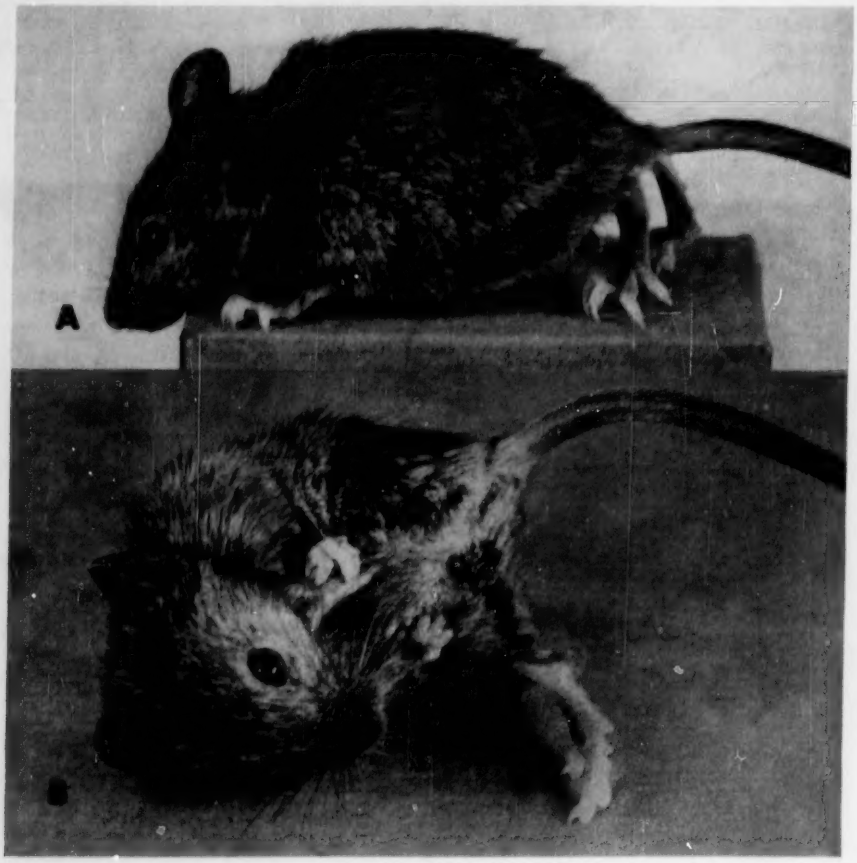

ATAXIC MICE

(SEE PAGE 77)

Mutant Barley

Eight Mosaic Mice

Four Species of Malaria

Lethal Genes in Honey Bees

VOLUME 46 MARCH-APRIL, 1955 NUMBER 2

The American Genetic Association

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THREE MOUSE MOSAICS

Figure 1

A—Mouse M-8-M is an inbred mouse of strain C3H$_f$. White hairs were not observed until the age of four months. *B*—Mouse H-1-M is a brown iebald with a tan nose. *C*—Mouse H-7-M is black with a brown spot in the belt region.

EIGHT MOSAIC MICE IN THIRTY YEARS

W. C. MORGAN AND S. P. HOLMAN*

WITH the accumulation of evidence indicating that somatic mutations may be induced[7, 8, 9] it becomes increasingly important to report observed spontaneous cases. The first seven mosaics to be reported here were observed in the mouse colony of the the junior author between the years 1928 and 1951; the eighth mosaic appeared in the senior author's colony during the period 1946 to 1953. It is estimated that an average of approximately 1200 pigmented mice per year were observed by the authors during this cumulative period of thirty years.

Reported Spontaneous Mosaicism

In 1926 Wright[10] reviewed the genetically analyzed cases of vertebrate color mosaics reported up to that time. Dunn[3] later described a case of mosaicism in the house mouse and discussed the 21 cases of rodent color mosaics, which included those of guinea pigs. Between 1926 and 1934 only four mouse mosaics were reported. Since then Feldman[5] has reported two mouse mosaics, and more recently Bhat[1] and Carter[2] have each reported a mouse mosaic. The comparatively rare occurrence of spontaneous somatic mosaicism in mice is evidenced by the sparcity of reports in the literature.

Observations

Table I describes the eight mosaic mice as to phenotype and sex. Progeny were saved from all mutants except M-8-M. The breeding program was such that mosaic mice were mated to their nearest available relatives. The matings were continued as sibships for at least two generations, and further in several instances. No F_3 mice with abnormal coat patterns were observed from mosaic progenitors. H-5-M and H-6-M were littermates. When mated together they produced normal appearing offspring.

Female M-8-M (Figure 1*A*) was an inbred mouse of strain $C3H_f$ in generation F_{40}. She was examined at monthly intervals for the presence of carcinoma of the mammary gland. Not until the third check, that is, at approximately four months of age, was the presence of white hairs observed. No intermediate shedding of hairs was observed.

Discussion

It has been pointed out by Dunn[3] that the frequent association between piebald and mosaicism can hardly be accidental. Fisher[6] reported on a tri-color mouse which was black and white with a "distinct chocolate dot between the right eye and ear." Three of the mosaics in the present study were brown piebalds with tan spots. Mouse H-1-M (Figure 1*B*) had a tan nose; mice H-5-M and H-6-M had tan spots located latero-dorsad. These mice constitute one of the larger categories and support the observations of Dunn[3] that mosaics occur more frequently in white spotted mice. Two possibilities are evident with these three mice. The first is that an easier detection of abnormal colors is permitted on a white background; the second is that the presence of piebald genes creates a less stable equilibrium—particularly during early embryogenesis.

Three cases of mosaicism are reported in belted (*bt bt*) mice. Female H-7-M and female H-2-M were homozygous for brown (*bb*) with tan and "cream" areas respectively. However, H-3-M (Figure 1*C*) was a black mouse with a brown spot in the belt region. This individual was similar to Fisher's tricolor mouse and may have been a heterozygote (*Bb*).

The color loci with which the mice in this report are concerned are listed in Table II. Inasmuch as several combinations in the multiple allelic *C*, c^i, c^{ch}, c^a, *c* series cause a dilution of brown color intensity, it is possible that five of the eight mosaics may be due to a change at that locus. On a non-agouti background, such as H-1-M, H-5-M, H-6-M, and H-7-M, a genotype of $c^{ch}c$ would cause a dilution of the brown color[4], such as the tan areas reported in Table I. Thus an original genotype of Cc^{ch}, in which a somatic cell had mutated from *C* to *c*, could result in the production of a "tan" area.

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An alternate hypothesis for these last four mice would be the possible somatic mutation of *D* to *d* in mice which were heterozygotes (*Dd*). Inasmuch as the *D* locus is relatively unstable when subjected to irradiation, (personal communication from Dr. W. L. Russell), it is suspected that the diminution in color intensity for these four tan areas may have been caused by the change $D \longrightarrow d$. However, it should be mentioned that the hairs in tan areas appeared to be darker brown than those of genotypically *aa bb dd* mice.

From several standpoints mouse M-8-M might be considered the most interesting. She not only had a latent expression, but also had diverging affected areas. With the possible exception of H-4-M, all of the other mosaics exhibited patterns which might be interpreted as having resulted from the early mutation of a somatic cell. However, to apply the same line of reasoning to M-8-M appears to be untenable, not only because of the latent period, but also because it would be necessary to postulate that several primordial cells mutated in a like manner (that is, from black agouti to white).

Inasmuch as the seven from the junior author's colony constitute only about half of the total number of mosaics which he observed (those with incomplete records having been omitted from this report), it is reasonable to assume that his colony contained families or lines with an inherited instability. That this situation may exist in related guinea pig families was reported by Wright[10].

TABLE I. Description of eight mice with somatic mosaicism

Text Identity	Phenotype	Sex
*H-1-M	Brown, piebald with tan nose.	f
H-2-M	Dilute, brown, chinchilla, agouti with "cream" area adjacent to white belt.	f
H-3-M	Black, belt mouse with brown area adjacent to white belt.	f
H-4-M	Yellow with black variegated pattern.	m
H-5-M	Brown, piebald with tan spot.	f
H-6-M	Brown, piebald with tan spot.	m
*H-7-M	Brown, belt mouse with tan spot in belt area.	f
*M-8-M	Black, agouti with dorsal and lateral white areas.	f

* Photographs included.

TABLE II. Color genotypes of the mosaics

Mouse	Genotypes	Probable Mutated loci
H-1-M	*aabbD-?? Bt — C-*	*C or D*
H-2-M	*A-bbdd-bbbc^{ch}*	*C*
H-3-M	*aaB-D-?-bbbt C-*	*B*
H-4-M	*A$^{?}$aBBD-?-Bt — C-*	*A*
H-5-M	*aabbD-??Bt — C-*	*C or D*
H-6-M	*aabbD-??Bt — C-*	*C or D*
H-7-M	*aabbD-?-bbbC-*	*C or D*
M-8-M	*AABBDDSSBtBtCC*	*?*

Many of the interpretations for somatic mosaics have been based on the likelihood of nondisjunction or a chromosomal loss by a primordial somatic cell. In Carter's[2] explanation, however, neither point mutation nor deletion satisfactorily account for breeding results. In addition to nondisjunction, he offers somatic reduction and somatic crossing-over as possible hypothetical solutions. Certainly mice H-1-M through H-7-M might be explained on the basis of an alteration of an early embryonic cell, but it would be more difficult to account for the latent period of M-8-M by resorting to any such hypothesis.

Summary

Eight new spontaneous mouse mosaics are reported. Extensive breeding tests of seven of these individuals produced negative evidence concerning germinal transmission. Six of the eight abnormal mice were homozygous for piebald or for belt. The appearance of several mosaics in similar lines of descent suggests the probability of an inherited somatic instability.

The eighth mosaic, which was from a highly inbred line, was unusual in that it involved a latent period of expression.

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A MUTANT LINE OF BARLEY INDUCED BY ATOMIC-BOMB RADIATION

The Effect of Partial Ovule Sterility on the Inheritance of Cream Seedlings

R. A. NILAN AND C. C. MOH*

A PRELIMINARY genetic analysis of barley mutants induced by atomic-bomb irradiation has been reported earlier.[2] Several lines were found which were characterized by the appearance of an unusually high proportion of recessive mutants in selfed progeny tests. Though extensive cytogenetical investigation of two of the lines, two distinct genetic mechanisms were found which satisfactorily accounted for the high frequency of occurrence of the mutants.[3, 4]

The present paper describes still another mechanism which results in an unusually high proportion of mutants among selfed progenies. It occurred in a mutant line characterized by plants which were partially ovule sterile and which produced on self-fertilization a high frequency of cream seedlings (a chlorophyll deficient mutant). Data will be presented to show that the high frequency of cream seedlings arises from the genetic consequences of the associated ovule sterility.

Materials and Methods

The mutant line described in this study arose from a population of 6-rowed barley (*Hordeum vulgare*, variety Trebi) which was subjected to atomic-bomb irradiation at Bikini in 1946. Following the irradiation, seeds of the X_1 generation were grown at Sacaton, Arizona. The following generations (X_2 to X_7) and the progeny tests of each generation were grown at Pullman, Washington. The method of conducting the progeny tests has been described previously.[3, 4]

Partially ovule-sterile green plants which produced on selfing a high frequency of cream seedlings were crossed reciprocally with Compana, a normal 2-rowed variety, to test the transmission of cream seedling and ovule sterility through male and female gametes.

The constitutions of the plants derived from self-fertilization and reciprocal crosses were determined by measuring the floret sterility in the spikes and by progeny tests.

Experimental Results

1. *Results of Selfed Progeny Tests*

Green, partially ovule-sterile plants, referred to hereafter as parental type, produced a high proportion of cream seedlings upon selfing. The proportion of cream seedlings observed in progeny tests of 340 parental type plants was 39.2 percent based on 12,922 out of 33,000 individuals. All cream seedlings died three to four weeks after emergence.

The ovule sterility of 33 parental type plants averaged 40 percent, based on 1,406 empty florets out of 3,500 examined. Pollen grains of these plants appeared normal in potassium iodide solution.

The green plants which constituted about 61 percent of the total F_2 from the parental type plants were of five genotypes as revealed in the next generation: 1) Partially ovule- sterile plants which produced a high proportion of cream seedlings (parental type); 2) fertile plants whose progeny derived from self-fertilization segregated 3 green : 1 cream seedling; 3) partially ovule-sterile plants which gave rise following self-fertilization to only green progeny; 4) fertile plants which gave rise to only green offspring; and 5) partially ovule-sterile plants which produced on selfing a low proportion of cream seedlings (average 4.5 percent). The frequency of these five genotypes are given in Table I.

*Assistant Professor and Assistant Agronomist and Former Research Assistant, respectively, Department of Agronomy, State College of Washington. C. C. Moh's present address, Division of Radiation and Organisms, Smithsonian Institution, Washington, D. C. Scientific Paper No. 1335, Washington Agricultural Experiment Stations, Pullman. Projects 1002 and 1068. This study was supported by Atomic Energy Commission Contract No. AT (45-1)-353 and funds provided for medical and biological research by the State of Washington Initiative Measure 171.

2. *Progeny Tests of F_2 Green Genotypes*

a. Plants Producing a Low Proportion of Cream Seedlings

As shown in Table I, there were four partially ovule-sterile plants producing a low frequency of cream seedlings. Three of these were propagated for further studies. After two generations of propagation, 508 plants were obtained. The five green genotypes which constituted these plants and their frequencies are presented in Table I.

The selfed progenies of 217 plants producing a low proportion of cream seedlings were counted. The proportion of cream seedlings among these progeny was 1,046/23,159 or 4.5 percent. The ovule sterility of the plants producing the low frequency of cream seedlings averaged 39 percent.

b. Fertile Plants Producing 3 Green : 1 Cream Seedling

About 11 percent of the green plants which were derived by self-fertilization from parental type were normally fertile and produced 3 green : 1 cream seedling. Additional progeny tests were conducted on 147 plants of this class. Each of these was fertile and 102 were heterozygous for cream seedling. The proportion of heterozygous and normal plants fits a 2 : 1 ratio by the chi-square test ($P = 0.3 - 0.5$).

c. Partially Ovule-Sterile Plants Producing Only Green Seedlings

The frequency of partially ovule-sterile plants among 527 mature plants which produced on self-fertilization only green seedlings was 301 or 57 percent.

3. *Transmission of Cream Seedling and Partial Ovule Sterility Through Male and Female Gametes*

The testcross plants which were derived from reciprocal crosses between plants of parental type and of Compana were green. Examination of the florets and progeny derived from self-fertilization revealed the following four genotypes: 1) Partial ovule sterility giving rise to green and cream seedlings; 2) fertile and producing green and cream seedlings; 3) partial ovule sterility producing only green seedlings; and 4) fertile and giving rise to only green seedlings. The frequencies of these four genotypes are given in Table II.

Four plants of genotype (1) gave rise to 13 percent cream seedlings in their progeny based on 40 out of 302 individuals. One hundred and twenty-five genotype (2) plants gave rise to 26 percent cream seedlings based on 3,126 out of 11,900 individuals.

When parental type plants as males were crossed with Compana females, the testcross plants were predominantly of genotypes (2) and (3). Furthermore, the frequencies of these genotypes were about equal, 44.3 percent (genotype 2) and 48.4 percent (genotype 3). On the other hand, when the parental type plants were the female parents the same two genotypes predominated among the testcross plants but were in frequencies of approximately 3 : 1, 71.7 percent (genotype 2) and 24.3 percent (genotype 3), (Table II).

4. *Germination Tests*

It has been reported[1] that the low germinability of the seeds of certain genotypes may result in deviations from normal genetic ratios. To test for such a phenomenon in the present study, seeds from 15 parental type plants were selected at random for germina-

TABLE II. Frequencies of genotypes of testcross plants from reciprocal crosses between parental type plants and Compana

	Producing green and cream seedlings		Producing only green seedlings	
Genotype	Partially ovule sterile	Fertile	Partially ovule sterile	Fertile
	Compana × parental type plants			
No. of testcross plants	1	54	59	6
Percent	2.4	44.3	48.4	4.9
	Parental type plants × Compana			
No. of testcross plants	1	71	24	3
Percent	1.0	71.7	24.3	3.0

TABLE I. A—Frequencies of green genotypes arising from self-fertilization of parental type plants. B—Frequencies of green genotypes arising from plants which produce a low proportion of cream seedlings following self-fertilization

	Producing high proportion of cream seedlings		Producing 3 green : 1 cream seedling		Producing only green seedlings		Producing low proportion of cream seedlings		Total
Genotype	Partially ovule sterile	Fertile	Partially ovule sterile	Fertile	Partially ovule sterile	Fertile	Partially ovule sterile	Fertile	
A									
Number of plants	352	0	0	50	31	1	4	0	438
%	80.4	–	–	11.4	7.1	0.2	0.9	–	100
B									
Number of plants	3	0	0	31	32	196	246	0	508
%	0.6	–	–	6.1	6.3	38.6	48.4	–	100

tion tests. Average germination of 960 seeds grown in the greenhouse was 96 percent. Thus, the high proportion of cream seedlings was apparently not due to the reduced germination of seeds of certain genotypes.

Discussion

The data demonstrate that partial ovule sterility and the occurrence of anomalous frequencies of cream seedlings in the progeny were closely associated characteristics of parental type plants. Plants which produced on self-fertilization either a high or low frequency of cream seedlings always possessed about 40 percent ovule sterility. Plants producing 3 normal : 1 cream seedling were always fertile. Furthermore, from the data (Table I) it is apparent that the abnormal frequency of cream seedlings among the F_2 progenies derived from self-fertilization can possibly be attributed to sterility in the ovules. Evidently, certain classes of female gametes were not functional.

This type of gametic abortion that only affects the ovules and not the pollen resembles in some respects the effect of lethal ovule, *lo*, in maize reported by Singleton and Manglesdorf.[7] Only about two percent of the *lo* ovules were functional while the pollen was completely normal. More recently Nelson and Clary[5] have reported another lethal ovule factor (lo_2) in maize which is transmitted only through the pollen.

Small pollen (*sp*) is another factor in maize that causes ovule sterility. Singleton and Manglesdorf[7] reported an average of 42 percent sterility for *sp* ovules. Similarly, Rhoades and Rhoades[6] reported 44 percent sterility of sp_2 ovules. Unlike the lethal ovule factor, the small pollen factor had an effect on the pollen which caused slow pollen-tube growth. No attempt was made in the present study to determine if a somewhat similar factor was operating to cause the ovule abortion in the mutant line of barley.

Although partial ovule sterility and production of cream seedlings were closely associated in parental type plants, they were not inseparable. The data in Table II show that about 7.4 percent crossing-over occurred between these two characteristics (in repulsion phase) when the parental type plants were the male parents.

The actual proportion of the four types of gametes produced by parental type plants (Table II) can now be determined. Assuming 7.4 percent crossing-over, the frequencies (Table III) of the four types of male gametes are $\frac{+\quad c}{+\quad +}$ 0.463, $\frac{s\quad +}{+\quad +}$ 0.463, $\frac{+\quad +}{+\quad +}$ 0.037, and $\frac{s\quad c}{+\quad +}$ 0.037 where *s* is the symbol for ovule sterility and *c* is the symbol for cream seedling. With the further assumption that two-thirds of the female gametes carrying *s* die, the four classes of female gametes are in the proportion of $\frac{+\quad c}{+\quad +}$ 0.695, $\frac{s\quad +}{+\quad +}$ 0.231, $\frac{+\quad +}{+\quad +}$ 0.056, $\frac{s\quad c}{+\quad +}$ 0.018.

Only five classes of plants occurred among the hundreds of progenies derived from self-fertilization of parental type plants (Table I). Plants homozygous for ovule sterility (*s*) did not appear.

The expected classes of genotypes and their frequencies derived from self-fertilization of parental type plants can now be calculated by combining the four classes of male with the four classes of female gametes in the respective frequencies as derived in the above paragraph. The observed values fit the expected very closely (Table IV). Similarly, the expected classes of plants and their frequencies derived from self-fertilization of the green plants which produced a low frequency (4.5 percent) of cream seedlings (Table I)

TABLE III. Change of gametic proportion as affected by partial ovule sterility (Assuming 7.4 percent of crossovers between *s* and *c*)

Genetic constitution of the parental type plant			$\frac{+\ c}{s\ +}$					
Types of gametes produced	non-crossovers				crossovers			
	+	*c*	*s*	+	+	+	*s*	*c*
Expected gametic proportion	0.463		0.463		0.037		0.037	
Expected gametic proportion when 2/3 of *s* gametes are lethal	0.463		0.154		0.037		0.012	
Resultant gametic proportion	0.695		0.231		0.056		0.018	

TABLE IV. Calculated and observed frequencies of genotypes derived from self-fertilization of parental type plants, $\frac{+\ c}{s\ +}$

Genotype	Phenotype	Calculated percentage	Observed percentage
$\frac{+\ c}{+\ c}$, $\frac{+\ c}{s\ c}$	cream seedling	40.6	19.2
	Green genotypes (*ca.* 61% of F_2)		
$\frac{+\ c}{s\ +}$	Parental type, partially ovule sterile, producing high frequency of cream seedlings	82.5	80.4
$\frac{+\ +}{+\ c}$	Fertile, producing green and cream seedlings in a ratio of 3 : 1	10.9	11.4
$\frac{+\ +}{s\ +}$	Partially ovule sterile, producing only green seedlings	7.1	7.1
$\frac{+\ +}{+\ +}$	Fertile, producing only green seedlings	0.4	0.2
$\frac{+\ +}{s\ c}$	Partially ovule sterile, producing a low frequency of cream seedlings	0.5	0.9

$\chi^2 = 3.0893$, $P = 0.3 - 0.5$

have been calculated and appear in Table V. Again the observed values fit the expected closely.

The close agreement between observed and expected in the two sets of data tend to strengthen the above assumptions and give credence to the hypothesis introduced, i.e., partial ovule sterility in parental type plants is the cause of the anomalous segregation of cream seedlings among selfed progenies derived from these plants. The exact nature of the ovule sterility has not been determined.

Summary

A mutant line of Trebi barley characterized by a high frequency of cream seedlings arising from partially ovule-sterile, green plants (parental type) was induced by atomic-bomb irradiation at Bikini in 1946. The ovule sterility of the parental type plants averaged 40 percent. No pollen abortion occurred in these plants. Following self-fertilization approximately 39 percent of the offspring from these plants were cream. The cream seedlings died during the first three to four weeks after emergence.

The green progenies (approximately 61 percent) derived from the parental type plants consisted of five genotypes which are described.

Parental type plants and plants of a normal 2-rowed variety (Compana) were reciprocally crossed to test the transmission of ovule sterility and cream seedling through male and female gametes. The results of these tests are described.

Ovule sterility and cream seedling were linked in repulsion by approximately 7.4 percent of crossing-over. Presumably, the high frequency of cream seedlings produced by the parental type plants was caused by the anomalous female gametic ratios resulting from the partial ovule sterility. Progenies homozygous for ovule sterility did not appear.

Based on the above assumptions of ovule sterility and the actual observations of 7.4 percent crossing-over the observed frequencies fit the expected very closely.

TABLE V. Calculated and observed frequencies of genotypes derived from self-fertilization of plants, $\frac{+}{s}\ \frac{+}{c}$, which produce a low proportion of cream seedlings

Genotype	Phenotype	Calculated percentage	Observed percentage
$\frac{+}{+}\ \frac{c}{c}$ or $\frac{+}{s}\ \frac{c}{c}$	cream seedlings	4.2	4.5
	Green genotypes		
$\frac{+}{s}\ \frac{+}{c}$	Partially ovule sterile, producing low frequency of cream seedlings	51.1	48.4
$\frac{+}{+}\ \frac{+}{+}$ or $\frac{+}{s}\ \frac{+}{+}$	Fertile, producing only green seedlings	38.4	38.6
$\frac{+}{+}\ \frac{+}{c}$	Fertile, producing green and cream seedlings in a ratio of 3 : 1	6.1	6.1
$\frac{+}{s}\ \frac{+}{+}$	Partially ovule sterile, producing only green seedlings	4.1	6.3
$\frac{+}{s}\ \frac{c}{+}$	Partially sterile, producing a high frequency of cream seedlings	0.3	0.6

$\chi^2 = 8.2425$, $P = 0.1 - 0.05$

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CHROMOSOMES OF THE FOUR SPECIES OF HUMAN MALARIA

Studied by Phase Microscopy

GORDON B. WOLCOTT*

IN *Plasmodium vivax*, the parasite of benign tertian malaria, the chromosome number is two in the asexual erythrocytic stages. One chromosome is about 1 μ long and the other shorter. Centrioles are present and during mitosis a spindle is formed. The chromosomes are Feulgen positive and have a coiled structure. The only exceptional condition is that the chromosomes remain condensed during a long resting stage of the nucleus, from the presegmenting stages to the mature trophozoite stage of the parasite, and neither a typical interphase nor a nuclear membrane is present. These observations were made on fixed and stained preparations.[6]

In the present study presegmenting and segmenting stages, with their chromosomes condensed, have been observed in the living condition using phase contrast microscopy. The number and morphology of the chromosomes of the four species of human malaria parasites and the association of the non-homologous somatic chromosomes are described.

Materials and Methods

Asexual stages of *Plasmodium vivax*, *P. ovale*, *P. malariae*, and *P. falciparum* were obtained from neurosyphilitic patients undergoing malaria therapy at the South Carolina State Hospital in Columbia, and the Georgia State Hospital in Milledgeville. Two strains of *P. ovale* were used, a Liberian strain and the Donaldson strain from the West Pacific area. The other strains were St. Elizabeth *vivax*, U. S. Public Health Service *malariae*, and McLendon *falciparum*.

The simplest method for obtaining blood for study was to make a deep finger prick and draw the blood from this into a white cell pipette which had been rinsed with a one percent solution of heparin. The blood was then transferred directly to the slides. For examination of wet preparations of blood under the phase contrast microscope using an oil immersion objective it is essential to have an extremely thin preparation. A drop of blood which would not quite fill the space under a 22 mm., number zero, coverslip was used. The preparation was usually further flattened by tapping it lightly. It was not necessary to seal the coverslip.

The possible effect of anti-malarial drugs on the morphology of the parasite (Thurston[4]) was avoided by using patients who had not been recently treated, or had not been treated at all.

The optical equipment used was a Bausch and Lomb microscope fitted with phase accessories. Illumination was from a 6-volt ribbon filament lamp using Köhler's method. For photographic work the General Electric Company photomicrographic lamp was also used. Wratten filters numbers 15 and 58 were used in combination.

The unretouched photomicrographs in Figure 2 were made at a magnification of 2000× using a 97× oil immersion objective and are here reproduced at a magnification of 3000×. The line drawings were prepared by inking photographic prints with India ink and removing the photographic image with 10 percent potassium ferricyanide followed by a water rinse and several minutes in 20 percent sodium thiosulphate. These were then transferred to drawing paper. The necessity for this procedure was that camera lucida drawings were impracticable because of the small size of the para-

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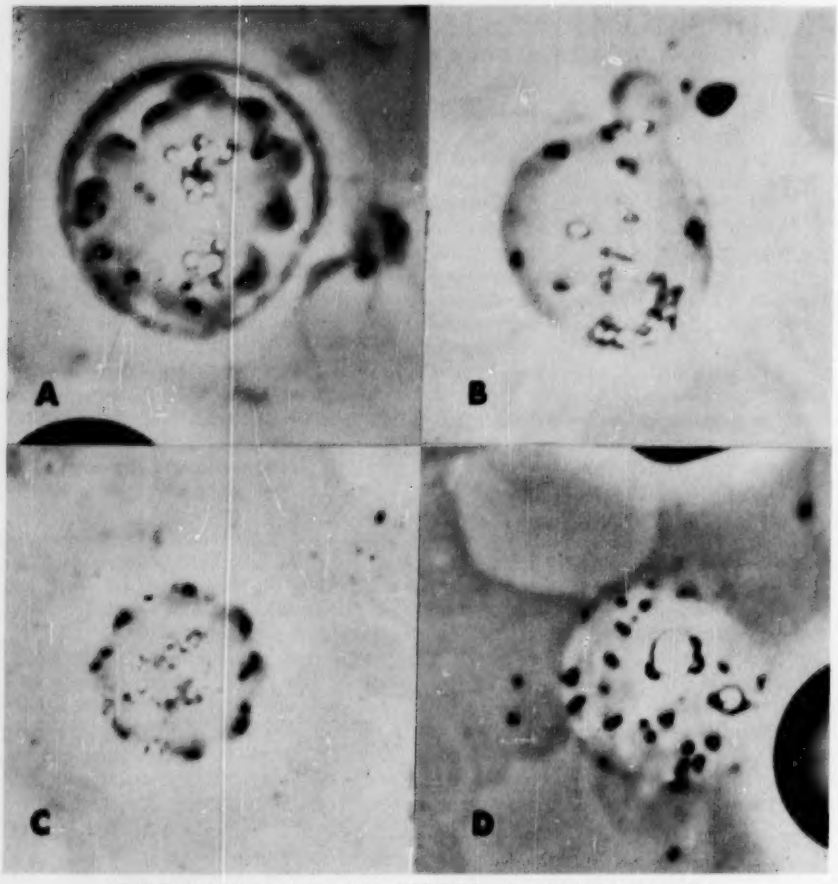


CHROMOSOMES OF FOUR SPECIES OF HUMAN MALARIA

Figure 2

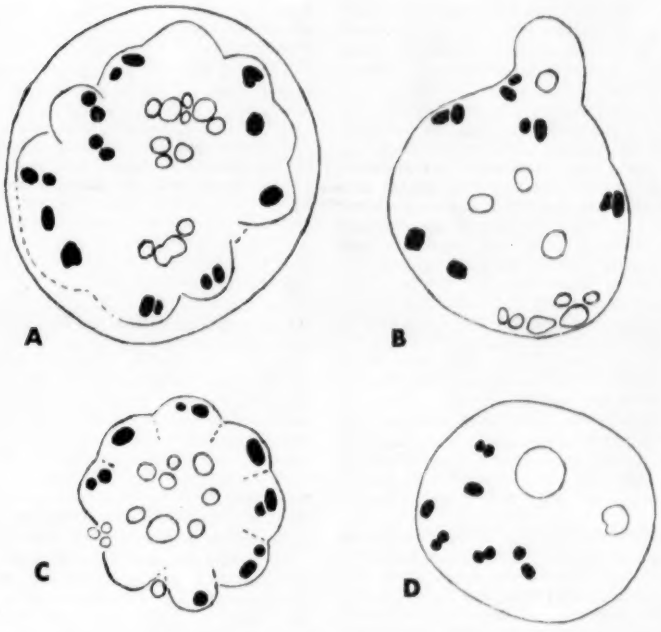
Photomicrographs of the chromosomes of the four species of human malaria parasite, using phase microscopy, ×3000. *A*—A parasite of *Plasmodium vivax* about to form merozoites. The outline of the host erythrocyte is still visible. *B*—A pre-segmenter of *P. ovale*. *C*—A segmenting schizont of *P. malariae*. By focusing it was possible to determine that each of the nuclei was composed of two chromosomes. *D*—A pre-segmenting stage of *P. falciparum*.

sites and because the parasites did not ordinarily remain alive for long periods after being mounted under a coverslip. Also, the chromosomes frequently shifted in position so that the appearance of the parasite did not remain constant.

A considerable number of free-hand sketches were made as a means of recording observations during the course of this study.

Observations

The largest number of observations was made on *Plasmodium vivax* and *P. malariae*. This was determined simply by the material available. In these two species literally hundreds of segmenting stages or presegmenters were observed. In most of these the chromosomes could be clearly seen. The chromosomes are always two in number with one chromosome about 1 μ long and the other one shorter. This is illustrated in *P. vivax* at the top of Figures 2*A* and 3*A*, and for *P. malariae* at the



PARASITES AND CHROMOSOMES

Figure 3

A-D—Parasites and chromosomes shown in Figure 2. The chromosomes are shown in black and the malarial pigment granules are shown in outline.

top of Figures 2*C* and 3*C*. Other nuclei in these illustrations do not give the same appearance because of the orientation of the chromosomes, the longest chromosome appearing as a dot when seen on end. Apparent variations in size of the chromosomes, as seen in the photographs, are also caused by differences in focus; chromosomes out of focus appear smaller. The chromosomes are usually lying parallel, as in the lower nuclei in Figures 2*A* and 3*A*, but move about, and may appear at an angle to each other, as seen in the nucleus at the upper left in Figures 2*A* and 3*A*. This movement of the chromosomes has been observed in unflattened parasites as well as in parasites such as those illustrated in Figure 2 which are partially flattened by pressure of the coverslip. However, at no time is the distance between the two chromosomes greater than the length of the smaller chromosome. When the chromosomes lie so close together that they cannot be resolved, or if one lies under the other, they appear as a single mass, even with the most careful focusing of the microscope.

The pigment appears in the photomicrographs as white circles or masses, usually toward the center of the parasite, and may be seen especially well in Figure 2*A*. When seen through the phase microscope the pigment appears refractile and orange in color and, though dark when out of focus, is easily distinguished from the nuclei.

The observations on *P. ovale* have been more limited because in *P. ovale* parasitemias are characteristically low and the infection was not at hand. The material studied was shipped, on ice, from Milledgeville via air express. The parasites seen were still alive as indicated by change in shape of the parasites and by movement of chromosomes during observation. Only five parasites of the Liberian strain and 15 parasites of the Donaldson strain of *P. ovale* in which chromosomes could be seen were studied. In all of these the picture was exactly the same and several nuclei in each parasite showed the two unequal chromosomes (Figures 2*B* and 3*B*). This pattern fits so nicely that observed in *P. vivax* and *P. malariae* that I consider these observations as

adequate to establish the chromosome complement for the asexual stages of *P. ovale*, both African and Pacific,* as being essentially similar to that of the other species of human malaria parasites.

One of the characteristics of *P. falciparum* infections is that, under ordinary circumstances, presegmenting and segmented stages do not occur in the peripheral circulation. In all of the species used in this study it was impossible to recognize the nucleus before the presegmenting stage. To obviate this difficulty skin scarifications were used to obtain segmenting stages.[3] Only a very few segmenters have been seen. Unfortunately no good photograph showing the unequal chromosomes has been obtained, but careful study of several nuclei leaves no doubt that the chromosomes are unequal in length, as in the other three species studied. Figures *2D* and *3D* are of a parasite about to segment.

The nuclei of the parasites of the four species studied were visible only during the later stages of schizogony. During these stages no nuclear membrane was visible; the nuclear material consisted only of the two chromosomes.

The undivided centrioles of *P. vivax* merozoite stages previously demonstrated in stained preparations[6] have been seen a few times during the course of this study, but not consistently. When they are present they are easily distinguished from the chromosomes by smaller size and lighter density. Also, though I have searched for dividing nuclei I have seen only two, both in the same parasite of *P. malariae*. The spindle was visible as a grayish body connecting the telophase nuclei.

The appearance of malaria parasites with the phase contrast microscope is strikingly different from their appearance in the usual air-dried films, fixed in methyl alcohol and stained with Giemsa. However, living and fixed presegmenting stages and segmenters agree closely within each species as regards such basic diagnostic features as relative size, number of nuclei or merozoites, and whether the host cell is enlarged or not.

Discussion

It is generally agreed that the four species of malaria under consideration are all closely related, though the exact relationships are not finally settled. It is not surprising, then, that the chromosome number and pattern are very similar in each. Because of the extremely small size of the chromosomes it is possible that there are minute differences in size or morphology between some of these species, but of such dimensions as to remain undetected with a light microscope.

The small number of chromosomes is a possible explanation of the similarity in chromosome complement of the species studied. Any loss or duplication of genetic material in a form with only two possible linkage groups would probably be lethal. If an alteration minute enough to survive has occurred it is undetectable.

The fact that the two chromosomes seen in human malaria parasites during asexual stages are of unequal length is a good indication that they are non-homologous and that the complement is haploid.[1] There is evidence from observations I have made on gametocytes of *P. vivax* and *P. falciparum* (as yet unpublished) which indicates that the gametocytes are also haploid and meiosis, therefore, postzygotic. The haploid condition of the nuclei studied in the present report has a direct bearing on their orientation.

As it seems reasonable that the chromosomes are haploid and non-homologous their association here is an unusual one. There is present some sort of attraction between non-homologous chromosomes in the somatic condition. This can hardly be considered as true pairing, as occurs in meiosis, but rather a loose association analagous to the well-known somatic pairing of homologous chromosomes seen in certain Diptera. The nature of this attractive force is, of course, unknown, as is that of attractive forces operating on homologous chromosomes in other organisms.

It should be pointed out again that the chromosomes usually lie parallel but may assume almost any relation to each other and are never separated by a distance as large as 1 μ. The different positions seen in the illustrations, and seen many times in living material, are not due to flattening or other distortion. This is clear from the fact that the relation of one chromosome to another may change during observation of nuclei and movement of the chromosomes has also been observed in unflattened parasites.

Previous studies of living asexual malaria parasites using phase microscopy by Trager,[5] Thurston,[4] and others report few observations on the nucleus. None of the workers report seeing chromosomes. Trager,[5] working with *P. lophurae*, noted that "Nuclear material cannot be seen except in very late segmenters in which the nuclei are barely visible as dark shadows against the lighter cytoplasm," an observation in line with my own. This indicates a change in optical path of the chromosomes or the cytoplasm, or both, during the growth of the parasite, with an increase in difference in optical path of the nucleus and cytoplasm. A possible explanation of this change may be found in the suggestion of Deane,[2] who studied the Feulgen reaction in *Plasmodium*, that ". . . a cyclic change in the relative concentrations of the two types of nucleic acid might occur, with the most desoxyribonucleic acid being present in the merozoites, less in the trophozoites. . . ." If this occurs it could very well account for changes in optical paths of the nucleus and cytoplasm resulting in the visibility, with phase, of the chromosomes during the late stages of schizogony.

Summary

Observations on the nuclei of *Plasmodium vivax, P. ovale, P. malariae,* and *P. falciparum* were made on living asexual parasites using phase contrast microscopy. The nuclei are visible only in the late stages of the asexual cycle. In all four species the chromosome number is two, with one chromosome about 1 μ in length and the other smaller. In the resting nuclei of late presegmenting stages and in merozoites there is no nuclear membrane and the chromosomes remain condensed. During this period the chromosomes usually lie parallel but may shift in position. They are at no time more than 1 μ apart. A constant association of non-homologous somatic chromosomes is described.

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GENETICS OF POPULATION STRUCTURE

THIS small volume* is an outcome of the symposium organized by Prof. Buzzati-Traverso of the Institute of Genetics, University of Pavia, under the sponsorship of the International Union of Biological Sciences, and held in Pavia, Italy, August 20-23, 1953, shortly before the opening of the Ninth International Congress of Genetics in Bellagio. It comprises a brief introduction, six original papers, some of which are followed by remarks of other participants, a section of "conclusions and perspectives," and a short closing address. All of the articles are well presented, with many good illustrations and tables. Although it is usually unnecessary to review individual papers in a publication of this sort, this volume is so packed with interesting experimental results and discussions that the reviewer would like to make brief mention of at least some of the highlights.

Results of selection with respect to the number of chaetae on the fourth and fifth abdominal sternites of *D. melanogaster* are reported by Alan Robertson (co-authors G. A. Clayton and J. A. Morris being absent). As selection continues beyond five or six generations to more than 20 generations, the responses of the various high and low lines become irregular according to conventional expectation. The various lines differ widely, and there is no satisfactory explanation for the permanence of large amounts of genetic variability for a trait that has been subjected to stringent selection for so many generations.

**Symposium on Genetics of Population Structure.* International Union of Biological Sciences Publications. Copies available at Liberia Internazionale Garzanti, Palazzo Universitario, Pavia, Italy. 141 pp. $2.30, paper bound.

Further work and analysis is now in preparation for publication.

Asymmetrical responses to upward and downward selection have previously been observed by other authors, but the results on selection for body-weight in mice presented by D. S. Falconer may prove to be a classical example. Even more important is his attempt to find a *genetic* explanation for the phenomenon in the asymmetry of the underlying genetic situation. Of the three forms of asymmetry in genetic systems—the scale of measurement, unequal frequencies of the alleles acting in opposite directions, and directional dominance—the first is shown not to be a chief cause of the differential response, and either the second or third, or a combination of these two factors, are shown to be quite adequate to explain the more rapid response to the downward than to the upward selection.

The third paper on selection effects is that of R. E. Scossiroli. In the usual situation a quantitative trait, responding to selection, will reach a "plateau" (the level at which the trait ceases to respond) in a sufficient number of generations of continuous selection. If the organisms are X-rayed and new mutations so induced, the trait may respond to selection beyond the usual plateau. Scossiroli's data with respect to selection on sternopleural hairs in *D. melanogaster* provide the most satisfactory piece of experimental evidence on this subject, supporting the conclusions that mutations do occur in polygenic systems, that they increase the genetic variability of the population, and that selection, natural or artificial, is able to utilize the new variability to produce lines with still higher plateaus.

Bruce Wallace's article on coadaptation and the gene arrangements of *D. pseudoobscura* is the longest and most technical, but is well organized and presented. Of the many problems he discusses, some are new and intricate, such as the optimal length of the inversion segments, patterns of association of the various gene arrangements, etc. It seems that within any one locality, there are usually only two predominating and coadapting gene-arrangements, while other types of arrangements, if they exist, are rare. (Theoretically this should be the case if one type of "inversion heterozygote" is greatly superior to others.) Wallace also suggests that the developmental processes of heterozygous individuals appear to be better buffered and more stable than those of homozygotes, and therefore, the heterozygotes have a greater adaptability to the chance variations of environment.

Only some of the participants in the ensuing discussion submitted their ideas for publication. Of these, Th. Dobzhansky remarks that the genotypes of individuals are integral parts of the gene-pool of the population, which is an organized system molded by natural selection. The inversion is an integrating agent in the complexes of polygenes, and therefore is of adaptive significance. Michael Lerner remarks that while the gene is the basic unit in *transmission*, it is not the unit in evolution and ontogeny. The simple mathematical models, dealing with changes in gene frequencies, may no longer suffice in dealing with the polygenic blocks, still less with the genotype. He also calls for clarification and precise definition of terms such as "homeostasia", "canalization", "genetic inertia", and "integration", and we could all easily add to this list.

As an example, Jens Clausen finds that after many years of crossing and breeding *Potentilla glandulosa*, petal width is controlled by at least six pairs of genes, some widening the petals, some narrowing them, some complementary to others, and some suppressing or hypostatic to others, with varying activities at different altitudes. Similar situations exist with respect to other characters. Clausen's explanation of this complicated situation is that the equilibriums that obtain in gene systems consisting of multiple genes of cumulative, complementary, and subtracting effect preserve great potentials of the population and so insure survival under changing conditions.

Harlan Lewis reports that the supernumerary chromosome(s) of *Clarkia* species is a duplication of part of the normal genome. The extra chromosome does not make the phenotype perceptibly different from that of normal plants. This shows how well adapted and buffered a phenotype is. Plants with additional chromosomes, however, seem to be more adaptable to arid regions. In connection with the above findings Carl Epling emphasizes the concept of a unified genotype, integrated by a multiple interaction of many loci; and he thinks that the findings in *Clarkia* also show that changes in the adaptive character of a population need not come about only by the gradual process of gene substitution. Structural modifications of a genome may also lead to a new polygenic system.

Buzzati-Traverso's "Conclusions and Perspectives" provides an excellent summary and discussion of the various concepts presented in the symposium. In the closing address J. B. S. Haldane praises the vitality of Italian science. With respect to the controversies that arose during the discussion, he says: "If we have not always agreed, we have at least seen clearly where we differ." Nothing better need be said of any symposium.

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CHROMOSOMAL VARIATION IN CHILEAN POPULATIONS OF DROSOPHILA IMMIGRANS

DANKO BRNCIC*

THE study of chromosomal inversions in natural populations of *Drosophila* has provided valuable information bearing on the problems of race formation. Quantitative and qualitative analysis of the gene arrangements found in the different areas of distribution of the species permits the establishment of phylogenetic relationship between the various populations. Moreover, inversion heterosis keeps adaptative gene combination protected from breakdown by recombinations.[6] The adaptive value of such internally balanced gene complexes, maintained in natural populations of many species of *Drosophila*, has been demonstrated through analysis of the natural populations themselves as well as through experiments in the laboratory.[3,5,6,9,10,11]

Comparative analysis of different species of the genus *Drosophila* has shown that, while some species exhibit a high degree of chromosomal polymorphism due to inversions, other species have no inversions at all.[16,21] Dobzhansky *et al.*[7] and Da Cunha *et al.*[4] have tentatively established a relation between the amount of adaptive polymorphism present in a population or a species, and the number and variety of the ecological niches which are under the control of that population.

It is important for a more complete understanding of the regularities in this field to compare the chromosomal polymorphism in different species adjusted to different environments. *D. immigrans* Sturtevant is at present a nearly cosmopolitan species which occurs mostly in association with man—in gardens, orchards, and fruit and vegetable stalls. However, in Chile it occurs also in natural habitats. Whether it is a species native to Chile is, for the time being, an open question. Up to the present *D. immigrans* has received little cytological study. Freire Maia *et al.*[14] have, however, published pictures of the salivary gland chromosomes, as well as some quantitative data on the gene arrangements found in Brazil.

Material and Methods

D. immigrans is a very widespread and common species in Chile. It has been found breeding on over-ripe fruit near towns, but also in natural habitats, such as woods, zones of xerophitic bushes, and even under the stringent ecological conditions of the desert. The distribution extends vertically from near sea level to altitudes above 1500 meters in the Andes. It seems that *D. immigrans* tolerates low temperatures, as it is one of the commonest species in spring and autumn collections, but rare during the summer.

Samples were collected in different habitats. The map shown in Figure 2 indicates the origin of the populations studied. Some samples were taken in desert regions, such as Azapa, where the average rainfall is under 0.1 mm per year. At Serena, Paihuano, and Rapel it rains about 100 to 120 mm a year, at Bellavista and San Vicente around 300 to 600 mm. In the southern rainforests, Valdivia, Ensenada, Puerto Varas, and Puerto Montt, the rainfall amounts to about 2,000 mm. yearly.

Quantitative data on chromosomal variations in the populations of the above-named localities were obtained by studying the salivary gland chromosomes of a single grown-up larva in the

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INVERSION HETEROZYGOTES

Figure 4

A and *B* shows the heterozygous inversions B in the right arm of the second chromosome. Compare with Figure 5 *A* and *B*. *C* shows the heterozygous inversion A in the left arm of the second chromosome. Compare with Figure 5 *C*.

progeny of each female collected in nature. For the analysis of the chromosomes, the usual method of squashing the glands in acetic orceine was employed. The gene arrangement found in a structurally homozygous strain from Azapa, Chile, was used as a Standard.

The notations used for the different chromosome strands by Freire-Maia *et al.*[14] will be used also in the present report.

TABLE I. Frequencies (in percent) of inversions found in heterozygous condition in *Drosophila immigrans*

Localities	Number of chromosomes studied	Without inversions	Inversions A	Inversions B	Inversions C	Number of heterozygous inversions per larva
Azapa (Arica)	53	86.8	—	13.2	—	0.13
Paihuano (Coquimbo)	37	83.8	—	16.2	—	0.16
Serena (Coquimbo)	19	89.5	—	10.5	—	0.10
Rapel (Ovalle)	22	77.3	—	22.7	—	0.22
Bellavista (Santiago)	27	63.0	18.5	18.5	—	0.37
San Vicente (O'Higgins)	40	87.5	7.5	5.0	—	0.12
Valdivia (Valdivia)	26	73.1	7.7	15.4	3.8	0.27
Puerto Varas (Llanquihue)	48	83.3	10.4	6.3	—	0.16
Ensenada (Llanquihue)	15	73.4	26.6	—	—	0.26
Puerto Montt (Llanquihue)	23	56.5	17.4	26.1	—	0.43
Total	310	79.3	7.4	12.9	0.3	0.20

TABLE II. Frequencies (in percent) of different gene arrangements in *Drosophila immigrans* in crosses between a Stanard strain from Azapa and stocks of various geographic origin

Localities	Number of chromosomes studied	Standard	A	B	C	B+C
Azapa (Arica)	20	95.0	—	5.0	—	—
Paihuano (Coquimbo)	20	65.0	—	35.0	—	—
Serena (Coquimbo)	20	90.0	—	10.0	—	—
Rapel (Ovalle)	20	90.0	—	10.0	—	—
Bellavista (Santiago)	20	90.0	5.0	5.0	—	—
San Vicente (O'Higgins)	20	—	—	100.0	—	—
Valdivia (Valdivia)	20	25.0	5.0	—	25.0	45.0
Puerto Varas (Llanquihue)	20	35.0	5.0	60.0	—	—
Ensenada (Llanquihue)	20	60.0	20.0	20.0	—	—
Puerto Montt (Llanquihue)	20	40.0	10.0	50.0	—	—

Variations in the Gene Arrangements

As in the Brazilian populations,[14] Chilean *immigrans* has a karyotype consisting of one pair of medium-length rods (X), one pair of V's (II), one pair of long rods (III) and one pair of short rods (IV). The Y chromosome is V-shaped. This karyotype is identical with that described previously by Metz and Moses.[15] The salivary gland chromosomes

INVERSIONS A, B AND C

Figure 5

A, *B*, and *C* represents the heterozygous inversions shown in Figure 4. *D*—The heterozygous inversion C in the right arm of the same chromosome.

have four long euchromatic strands and one euchromatic dot, as can be expected from the configurations in the metaphasic plates.

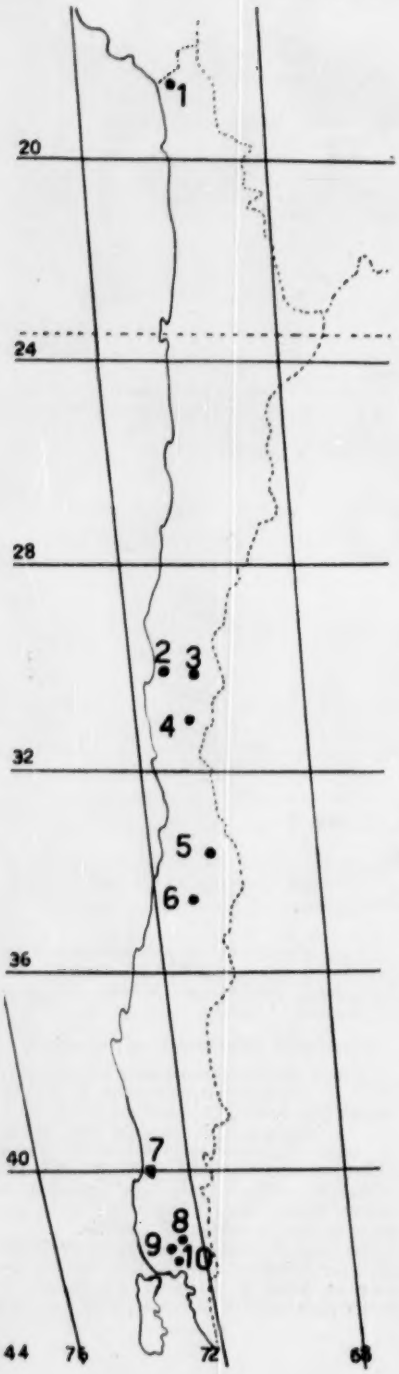
No inversions have been found in the first (X), third or fourth chromosomes. In the left arm of the second chromosome one inversion has been observed, and in the right arm two more were seen. The inversion in the middle part of the left arm, designated here as "Inversion A" (Figure 4*C* and 5*C*), is the only inversion reported by Freire-Maia in Brazilian populations of *D. immigrans*. The gene arrangement B gives a relatively small subterminal inversion at the distal end of the right arm of the second chromosome. (Figure 4 *A* and *B*, and 5 *A* and *B*). The small inversion C lies in the proximal part of the right arm of the same euchromatic strand. (Figure 5 *D*).

As all the inversions are independent of each other, it is not possible to establish the phylogenetic relationships between the gene arrangements involved.

Geographic Distribution of Inversions

Table I summarizes the data on the incidence of heterozygous inversions in the 10 populations studied. It must be pointed out that the inversion B is the only one, besides the Standard gene arrangement, which is distributed throughout Chile. Inversion A is restricted to southern Chile from Bellavista to Puerto Montt. Inversion C seems to be endemic in the population of Valdivia.

The mean frequency of heterozygous inversions per individual is about 0.20, exactly the same as found in Brazilian populations by Freire-Maia *et al.*[14] However, only one kind



of inversion is found in Brazil, while in the Chilean populations three inversions are found. In Chile, the widely distributed inversion B has a medium frequency of 0.13 per larva.

The data in Table I show only the distribution and incidence of inversion heterozygotes. Table II summarizes the results of the crosses of the Standard strain to strains from the different populations studied. It is evident that in the different parts of Chile the populations are homozygous for different gene arrangements. This is especially clear for the gene arrangements in the left arm of the second chromosome. Homozygotes for the Standard gene arrangement are most frequent in northern Chile, while the gene arrangement B seems to be most abundant, or at least as abundant as Standard in southern Chile. The arrangement C, alone, or in combination with B is frequent at Valdivia.

Discussion

Studies on chromosomal polymorphism in *Drosophila* have shown that, while in some species like *D. virilis*[17] and in several members of the *repleta* group,[21] the gene arrangement is extremely stable, in other species there is quite a number of varieties due to chromosomal inversions. The gene arrangement may be equally variable in all the chromosomes, as in *D. melanogaster*,[12] *D. ananassae*,[13] *D. robusta*[2] and *D. willistoni*.[3] In other species the inversions are concentrated in one chromosome, as in *D. pseudoobscura*,[8] *D. nebulosa*,[18] *D. melanica*[20] and *D. guaramunu*.[1] Though the number of inversions known in *D. immigrans* is small, all of them are found in the second chromosome.

Dobzhansky *et al.*[7] and Da Cunha *et al.*[4] have shown that in several species of *Drosophila* there exists a correlation between the amount of the chromosomal polymorphism and the diversity of the habitats in which a population lives. The greater the ecological versatility of a population, the greater the chromosomal polymorphism, and vice-versa. The distribution of the gene arrangements in *D. immigrans* is, then, very instructive. In the populations from northern Chile, which live under the stringent ecological conditions of the desert, only the Standard and B gene arrangements are found. On the other hand, in the South, where the species occupies the rich habitats of the rainforest, there are at least three different genetic arrangements beside Standard. It should be pointed out that *D. immigrans* is not a strictly domestic species, like *D. melanogaster*. As shown in Ta-

GEOGRAPHIC LOCATION OF *D. IMMIGRANS*

Figure 6

Map showing the collecting localities of *Drosophila immigrans* in Chile: 1. Azapa. 2. Serena. 3. Paihuano. 4. Rapel (Ovalle). 5. Bellavista. 6. San Vicente. 7. Valdivia. 8. Ensenada. 9. Puerto Varas. 10. Puerto Montt.

ble II, the Standard gene arrangement is the most frequent in the population from northern Chile. On the other hand, in the central and southern part of the country there is a high incidence of the B arrangement, while at Valdivia, C, alone, or in combination with B, is most frequent. Even these preliminary results indicate clearly the existence of racial differences between the geographical populations of *D. immigrans*. These racial differences arose evidently in response to the different ecological conditions, and are maintained by a geographic isolation between the populations.

Summary

Chilean populations of *D. immigrans* have been analyzed for variations in the gene arrangements in the chromosomes. Besides the Standard, three different gene arrangements have been found in the second chromosome. One of them is identical with that described by Freire-Maia from Brazil. Although the mean number of heterozygous inversions per individual is low, it seems possible to establish a relationship between the type of the habitat and the chromosomal polymorphism: Only two gene arrangements are found in the deserts of northern Chile, while four gene arrangements occur in the rainforests of southern Chile. Although *D. immigrans* is to a certain extent a domestic species, it forms local populations, races, which differ from each other by the gene arrangements in their chromosomes.

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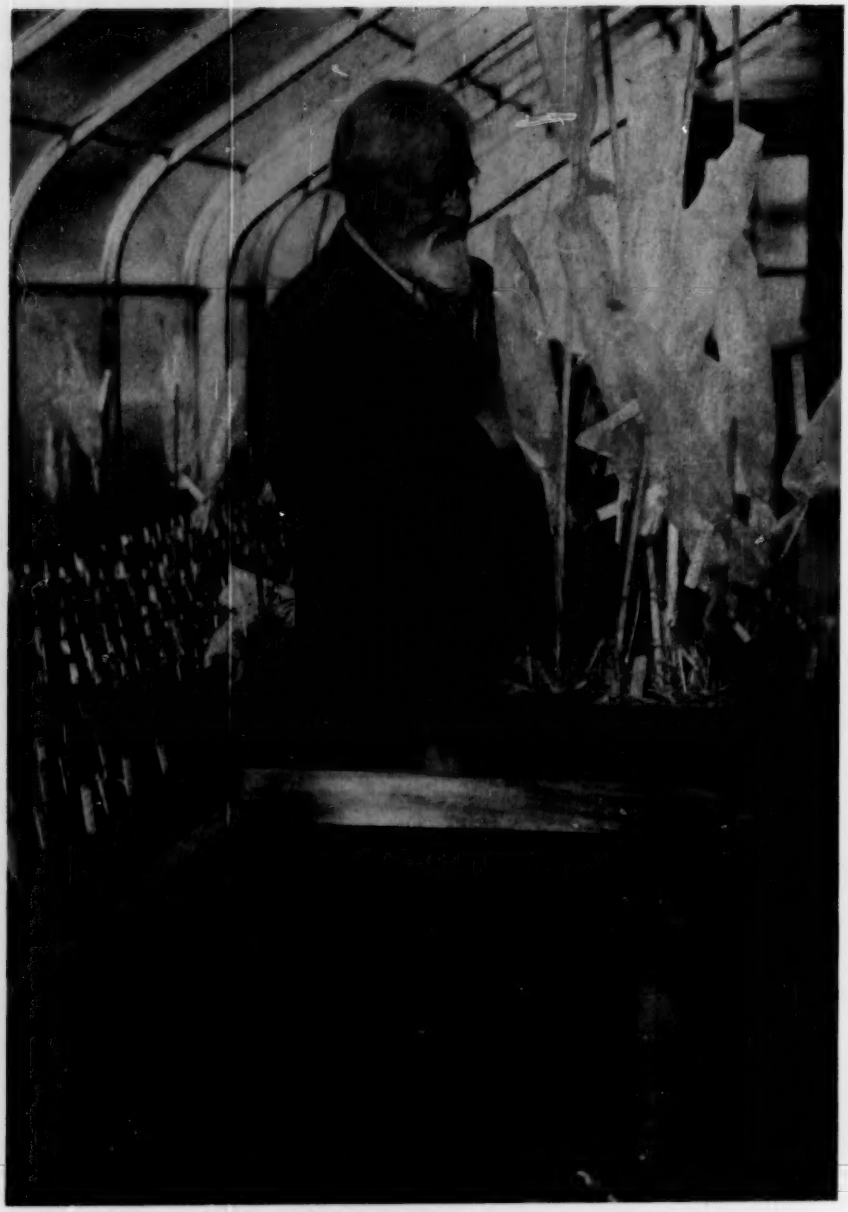

GEORGE HARRISON SHULL

GEORGE HARRISON SHULL

1874—1954

SINCE last September, genetics has lost three of its pioneer investigators all of whom started their work a few years after the rediscovery of Mendel's laws. Dr. George Harrison Shull of Princeton, the first of the three to die, passed away on September 29, 1954, after a long illness. He was born and brought up in rural Ohio where his parents were quite poor and where his early formal education was very inadequate, but he had a great desire for knowledge and great industry and application. He more than made up for his poor schooling by intensive home study. He was about ten years old when he first became interested in plants and about 16 when he decided to make botany his life work.

At the age of 18, Dr. Shull began a five-year period of teaching in several small public schools in Ohio at times handling seven different grades each day. In 1897 at the age of 23, he started as a full-time student at Antioch College. He was given free tuition but supported himself otherwise by serving as custodian of laboratories and the library, as engineer in charge of the heating plant, and as head janitor and college plumber. During much of his college career he got up at four o'clock in the morning and went from house to house firing furnaces. Obviously such strenuous work left no time for sports or for frivolity, and only a person of strong character and fixed purpose could have continued his studies under such circumstances. In later life, this strong character was frequently evident. He had a strict sense of right and wrong and a stern sense of duty and was never willing to compromise or to yield on any point if he felt that he was in the right. He was kindly but firm both with his family and his students. He was always fair and just but he expected to do his duty and to fulfill his obligations and his promises and he demanded the same treatment from others. When the writer was a junior in college, just after the beginning of the fall term, Dr. Shull appeared late for his laboratory in genetics. With boyish glee, the class decided to follow the Princeton custom of walking out of class if the professor did not appear within a certain time. The next time the class met, Dr. Shull expressed his disappointment and in kindly, calm, but firm tones informed the class that he expected the laboratory to be made up. It was. He never raised his voice in anger, but his quiet expression of disapproval had more effect than the blustering and rantings of many another professor.

After Antioch, he went to the University of Chicago for graduate work. As a senior at Antioch he had become interested in biometry and had made an extensive study of variation in wild asters. He was fortunate, then, to find the late Charles B. Davenport teaching biometry at Chicago. Dr. Shull received his Ph.D. degree in Botany and Zoology in March, 1904, writing up some of his aster work as his thesis. Between the time he graduated from Antioch and the completion of his work for the doctorate he spent 10 weeks in eastern Tennessee with an expedition making a forest survey for the U. S. Bureau of Forestry; three months in the U. S. National Herbarium as a Botanical Assistant; and two summers with the U. S. Bureau of Plant Industry, making a study of the plants used as food by ducks to try to learn the causes of the depletion of wild ducks in the Chesapeake Bay. During this period he published several papers, the first of which appeared in 1891 when he was seventeen years old. He was quite interested in buds and their development and published a half dozen papers on them. These earlier papers were published largely in the University of Chicago's *Botanical Gazette*, and he wrote a large number of book reviews for that journal.

His eleven-year period at the Carnegie Institution for Experimental Evolution was marked in its earlier years by prolific work on the inheritance of numerous traits in a large number of different plants. This was a period in which he, like many others, was testing out the newly rediscovered Mendelian principles and trying to find material for a life-time research program. He finally settled on corn, which he abandoned in 1915, and

Oenothera and *Capsella*, which he continued until his retirement. During this period he made his great discoveries in hybrid vigor which ultimately revolutionized corn farming methods and earned him many signal honors in the last decade of his life. From 1906 to 1911, the Carnegie Institution sent him to California for half of each year to study and evaluate scientifically the work of Luther Burbank. During his Cold Spring Harbor period he married twice. In July, 1906, he married Ella Amanda Hollar who died ten months later. In August, 1909, he married Mary Julia Nicholl, who survives him along with their six children.

From 1915 to 1942, he held a professorship at Princeton University where he regularly taught elementary genetics in the Autumn and beginning botany in the Spring. One of his chief joys was to take his botany class on trips through the pine barrens and sand dunes, through land which he was years later to be instrumental in having preserved as a wild life sanctuary under the National Park Service. He fought long and courageously and was very proud to have been largely responsible for the preservation of the last remaining undeveloped dune land in that part of the country. It was always his regret that he never had many graduate students since Princeton offered few courses in botany.

Dr. Shull was the founder and first editor of *Genetics* and the first editor of the Genetics Section of *Botanical Abstracts*. He was active in many scientific societies and was president of the American Society of Naturalists in 1917 and of the Torrey Botanical Club in 1947. He was the first president of the Princeton Chapter of Sigma Xi which he was largely instrumental in organizing in 1932. He was a member of the American Philosophical Society and of a number of American and foreign societies such as the Deutsche Botanische Gessellschaft, the Academy of Science of Vienna, the Deutsche Gesellschaft für Vererbungswissenschaft and the Société Linnéenne de Lyon. During the last 10 years of his life his early work in heterosis in corn won him five awards which included the Marcellus Hartley Medal of the National Academy of Sciences and his inclusion in Popular Mechanics's list of the 50 most important men in science and engineering from 1902 to 1952.

Dr. Shull's philosophy of life might be illustrated by several quotations. In the memorial minute presented to the Princeton University Faculty on November 1, 1954, it is stated: "He was always kindly and took infinite pains with the interested student, but his own stern code sometimes required corrective measures of the lazy or inattentive." In a talk which he gave to the Princeton Old Guard on October 9, 1946, the following interesting statements appear: "The context of the Declaration of Independence makes it clear that * * * all men are created equal in their right to be true to their own nature, in other words their right to be different from every other individual in the world." "My time for work, my time to do a good deed, my time to encourage my neighbor and to exert a salutory influence on the lives of those about me *is the present moment.*" "I hold as the most fundamental working hypothesis I can conceive, that *we are living in a planned world.*" "Since it is an obvious part of the Great Plan that death come to all men, I look forward to that experience with a calm belief that it is the greatest adventure in life, a blessing not to be sought prematurely, but to be welcomed in the spirit of William Cullen Bryant's Thanatopsis."

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Corrigendum

In the article "Seed Development and Failure in Horseradish," Vol. 46, pages 15-21, two errors appear. Second Column, page 16, paragraph 1, line 5, the word gametes should be singular and would read as follows: "The egg and the other male gamete fuse to form the zoygote." The caption to Figure 12, page 20, should read: "Triple Fusion Nucleus," not nucellus.

BLACKBERRY—RASPBERRY HYBRIDS

GEORGE M. DARROW*

AMONG the finest flavored varieties in the raspberry-blackberry group are hybrids between these two fruits and derivatives from them. Interest in crossing these two related berries has continued from as far back as 1881 to the present. Evidence has gradually accumulated to indicate that such crosses can be successful. Some results of crosses between a diploid blackberry and diploid raspberries and tetraploid blackberry and tetraploid raspberries are reported here.

Previous Blackberry × Raspberry Hybrids

In the United States the first four reported raspberry × blackberry hybrids were the Logan (Loganberry), Phenomenal, Primus, and Paradox. Investigations by Crane and Thomas[4] and Waldo and Darrow[12] indicate that the Logan (6*x*), raised from seed by Judge J. H. Logan in 1881, actually resulted from a cross of the octoploid Aughinbaugh variety of the Pacific Coast trailing blackberry and the diploid Antwerp European raspberry. In this hybridization a diploid pollen grain from the raspberry appears to have taken part. The Logan is an amphiploid, its seedlings are fertile and they resemble the Logan, not segregating toward the raspberry nor the trailing blackberries.[6] The Phenomenal (6*x*), originated by Burbank, is also a blackberry × raspberry hybrid of similar origin (an Aughinbaugh × Cuthbert segregate) according to Burbank.[13] Primus was also reported by Burbank as a cross of the Aughinbaugh and Siberian raspberry, *Rubus crataegifolius* Bunge. Burbank[1, 2, 13] also reported that he had produced hybrids of Lawton blackberry (presumably 4*x*) with Golden Queen raspberry (2*x*) and of Crystal White blackberry (2*x*) with Shaffer raspberry (2*x*). Though most seedlings of the last cross were partly or wholly sterile, a productive one with light red berries was named Paradox by Burbank.

In Texas the tetraploid Nessberry was derived from a cross of a selection of the diploid southern dewberry, or trailing blackberry (*Rubus rubrisetus* Rydb. = *R. trivialis* Michx.), with the diploid Brilliant red raspberry.[10] The first seedlings of the cross were nearly sterile and presumably diploid, but in the third generation the productive seedling named Nessberry—which proved to be tetraploid appeared.[14] It has not succeeded as a variety because the fruit does not separate readily from the receptacle or the stem.† Yarnell[14] later crossed the Nessberry (4*x*) with the dewberry (2*x*) and obtained fertile diploids. Three of these were named Earliness, Bigness, and Regalness. Though they resemble the dewberry, *R. trivialis*, they are considered by Yarnell to have genes from the raspberry.

B. M. Young, in Louisiana, originated the Young variety (6*x*) from a cross of the Phenomenal (6*x*) with the Mayes dewberry.[7] The Boysen (6*x*) introduced in 1933, is so similar to the Young that it must have had a similar origin. G. F. Waldo crossed octoploid selections of the native trailing blackberries with the tetraploid red raspberry La France and obtained several hundred seedlings of the general type of the Logan. He also has hybrids of Zielinski (12*x*) × Logan (6*x*), of Black Logan (6*x*) × Young (6*x*), and of Boysen with various hybrids. He named the finest flavored of all these hybrid berries the Cascade (9*x*), from the cross Zielinski (12*x*) × Logan (6*x*).

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†B. M. Young, originator of the Young dewberry, suggested to the author that by selecting blackberry or dewberry parents with fruits that separate very easily when picked, this difficulty could be overcome.

BLACKBERRY-RASPBERRY HYBRIDS
Figure 7

A—Fruit cluster from highly sterile plant; *B*—Fruit cluster from fruitful plant (No. 2-242); *C*—Pistillate to flower cluster typical of the majority of the seedlings.

In 1951 the Armstrong Nurseries of southern California patented the Magnaberry, which is a productive F_3 derived from a cross between Nessberry ($4x$) and the Sodus raspberry ($2x$). It is said to bear fruit comparable in size with that of the Boysen and to propagate by rooting at the tips of the new canes. It is thought to be a tetraploid. If so, a chance diploid pollen from the raspberry must have fertilized the diploid egg of Nessberry.

In Europe a triploid is widespread and common in the wild and is considered to be a hybrid between the raspberry *R. idaeus* L. ($2x$) and the trailing pseudogamous blackberry *R. caesius* L. ($4x$).[9] This triploid rarely produces seed, reproduces by rooting at the stem tips, and forms immense thickets. Gustafsson considered *R. caesius* itself an apomictic triple-hybrid blackberry derived from blackberry, raspberry, and *R. saxatilis* L. The breeding behavior of the western trailing blackberry, particularly of *R. ursinus* Chame & Schlecht., in crosses with the red raspberry, indicates that it has a set of red raspberry chromosomes in its ancestry and its resemblance to *R. caesius* also suggests this.

In England the Mahdiberry ($3x$), a hybrid between the common English wild blackberry (*Rubus rusticanus* (E. Merc.), $2x = 14$), and the Belle de Fontenay ($4x = 28$) raspberry, and the Laxtonberry ($7x$)—a hybrid between the Logan ($6x$) and the Superlative raspberry ($2x$)—and the Veitchberry ($4x$)—a self-fertile hybrid of the native English blackberry ($2x$) with the November Abundance ($4x$)—have been named. However, they have not succeeded commercially because their fruits do not separate readily from the stems. Crane and Lawrence[3] state that the Mahdiberry and Laxtonberry, with odd numbers of chromosome sets, are not so fertile as the Veitchberry, with an even number. In Hungary, Porpaczy[12] crossed the Lloyd George raspberry ($2x$) with the European dewberry ($4x$) (*Rubus caesius*) and then crossed the best seedlings of this parentage with the Logan. The resulting hybrids were of two types, one with fruit like the Logan ranging from bright red to dusky black and the other like a "tremendous raspberry" and dark red to black. Porpaczy named the hybrid *Rubus mohacsyanus* Porpaczy, (*Rubus idaeus* × *R. caesius*) × *R. loganobaccus* Bailey (*R. ursinus* × *R. idaeus*).

The commercial success of the varieties Logan ($6x$), Phenomenal ($6x$), Boysen ($6x$), Young ($6x$), Cascade ($9x$), and Olallie ($6x$) in contrast to the poor success of the European Mahdi-

RASPBERRY, BLACKBERRY AND HYBRID LEAVES

Figure 8

A—Pinnate red raspberry leaf; *B*—Palmate Early Harvest blackberry leaf; *C*—Pinnate-palmate leaf typical of the hybrids between the Early Harvest blackberry and red raspberries.

berry (3*x*), Laxtonberry (7*x*), and Veitchberry (4*x*) and of the American Paradox and Nessberry (4*x*) prompted a few workers to make further crosses between raspberries and blackberries. Besides making the cross *R. trivialis* (2*x*) × Brilliant (2*x*), which resulted in the Nessberry, Ness also crossed *R. trivialis* with the diploid Haymaker raspberry. In Texas, following up the work of Ness, Yarnell[14] made diploid × diploid crosses between these fruits but Crane and Thomas in England[5] stated that they had produced no direct diploid hybrid between the raspberry and the blackberry. In 1953 Einset and Pratt[8] reported crossing diploid and tetraploid red raspberries with the tetraploid blackberry Eldorado. They obtained about 25 triploid and tetraploid hybrids. Of these the triploids were sterile, and at least one tetraploid (Hailsham red raspberry (4*x*) × Eldorado (4*x*)) was fertile.

Diploid Blackberry × Diploid Raspberry

Here at Beltsville, Md., in crosses between blackberry and raspberry, the diploid erect-growing blackberry Early Harvest was the seed parent in crosses of the red raspberry variety Taylor and three red raspberry selections (two resulting from Lloyd George × Ranere and one from Newburgh × Lloyd George), all diploid. The crosses were made in 1939 and the seedlings were planted in 1941. Of these 49 flowered in 1942. They were grown in a field containing hundreds of seedlings of varieties of blackberries and raspberries and hence had ample opportunity for pollination.

All seedlings of the crosses listed had erect shoots. Most were more vigorous and had darker green leaves than either parent. Of 43 survivors on which records were taken, only one (No. 2-42) was fertile and productive and it was saved. A second seedling was fertile and productive in 1942, but it died that year. The berries of both seedlings resembled those of the Young, Boysen, and Nessberry in color and high flavor, but were smaller. The berries did not pick off easily, just as in the similar fertile hybrids, Nessberry and Veitchberry.

The surviving productive plant (No. 2-42) (Figure 7 *B*) suckered freely and was much less thorny than the Nessberry. Dr. Haig Dermen found it to be a triploid and an open-pollinated seedling of it to be a pentaploid. In later years this selection (No. 2-42) was severely dwarfed, presumably by a virus disease, and was discarded. A notable characteristic of the hybrid seedlings was that although both parents produced sucker plants very freely, only three of the seedlings suckered at all freely. In 1943 these had 10, 14, and 26 suckers, respectively. Twenty-six seedlings produced no suckers, seven produced only one, three produced only two, and four produced several suckers. Though the fertile seedling suckered freely, a row of 34 open-pollinated seedlings of this one produced only two suckers.

A second notable characteristic of the hybrids was their flower types. Both the blackberry and the raspberry parents were hermaphrodites. However, of 49 seedlings alive in 1942, 20 had flowers that were hermaphrodite in appearance, while 29 had either pistils only, or pistils and various types of abortive stamens. This is in contrast to the crosses of the hermaphrodite blackberry Ideal Wild (8*x*) with La France raspberry (4*x*), in which all

59 seedlings that bloomed had hermaphrodite flowers.[13]

Of the 49 seedlings none was very prickly, but most had small, soft prickles. Three had no prickles. The productive selection surviving to 1943 had relatively few small prickles. In comparison with these Early Harvest × red raspberry seedlings, the Nessberry is extremely prickly, more so than any of these seedlings.

Further observations were made on 43 of the original 49 seedlings. The large leaves of 19 seedlings were pinnate-palmate; in 11 seedlings the leaves were ternate, in four they were palmate, and in nine they were pinnate (Figure 8). As pinnate-palmate leaves are produced only by plants of great vigor, it is possible that most seedlings would have shown pinnate-palmate leaves. The leaves of Early Harvest are pubescent and green on the lower surface, while the red raspberries are whitish tomentose below. Leaves of 33 seedlings were green below, while those of 10 were whitish but intermediate between the leaves of the parents.

A third notable characteristic of the hybrids was their disease resistance. The Taylor red raspberry is quite subject to leaf spot and anthracnose, being entirely defoliated by leaf spot in 1942; but on the two observed seedlings of hybrids between it and Early Harvest, no leaf spot or anthracnose appeared. Only five of the 43 seedlings had leaf diseases of any kind and only five had any anthracnose. Yet, pure red raspberry seedlings were badly affected by both leaf spot and anthracnose. Sixty-three open-pollinated seedlings were raised from the productive surviving selection (No. 2-42). They showed no common leaf spot nor anthracnose, but a few had some leaves infected with *Cercospora* sp.—the cause of southern leaf spot.

If raspberry-blackberry hybrids habitually have such resistance to leaf spot and anthracnose and such hardiness and vigor of plant as did most of these hybrids and if fertile seedlings can be regularly procured, promising new varieties with high-flavored berries may be obtained. Many seemed hardier than either parent. Resistance to disease may have been a factor in their hardiness. The major drawback was the difficulty in picking; the berries neither picked off like blackberries nor pulled off like raspberries.

Tetraploid × Tetraploid Crosses

In 1943 the Colossus (4*x*) and Hailsham (4*x*) red raspberries were pollinated with the blackberry selection No. 459 (Eldorado × self) (4*x*). In 1945, 82 seeds were sown and seven seedlings were raised. These seven seedlings were true hybrids and were moderately vigorous, but since they were set in a poor location in the field, they were finally lost. The somatic chromosome number of one of these was determined by Dermen to be 4*x* = 28. The few berries observed did not separate readily from the stem or receptacle.

Discussion and Summary

Seedlings resulting from crosses between the diploid erect-growing blackberry Early Harvest and diploid red raspberries were vigorous—some were extremely vigorous. They had three notable characteristics: (1) most of the seedlings were nonsuckering, though both parents suckered freely; (2) over half were pistillate, though neither parent was pistillate; (3) the leaves of 38 were free from any leaf disease. The canes of only five out of 43 had any anthracnose up to the time they were discarded though red raspberry seedlings planted among them were badly affected. Most of the seedlings had bristles but none was very prickly. More seedlings had intermediate-type leaves than had either pinnate (raspberry type) or palmate (blackberry type) leaves. The leaves of the under surface of 33 seedlings were green and 10 were whitish, but intermediate between the leaves of the parents. Crane and Thomas[4] pointed out that the chromosomes of diploid raspberries and blackberries can pair with little restriction but are sufficiently differentiated to compel self-pairing when there are two sets of each in the hybrid. The two fertile seedlings obtained in our work had fruit that did not separate from the stem or from the receptacle and hence in themselves were of no commercial value.

In order to obtain useful varieties with fruits that do separate like either the raspberry or the blackberry, there should presumably be an uneven balance of blackberry and raspberry chromosome sets or, as suggested by B. M. Young, the fruit of the blackberry parent should separate very easily from the stem. When several fertile hybrids with an even balance of chromosome sets are available for selfing or intercrossing, seedlings with berries which separate easily from the stem may segregate. In addition to crosses between 8*x* blackberries and 4*x* raspberries, crosses should be tried between 12*x* blackberries and 4*x* raspberries. Even in the crosses between octoploid blackberry and tetraploid raspberry reported by Waldo and Darrow[12] it is still difficult to separate the berry from the stem. This difficulty may be overcome if further progenies are raised from the fertile hybrids. The greatest need is for hardy tetraploid red raspberries as well as hardier octoploid and 12-ploid blackberry varieties to use in this type of breeding.

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ARTIFICIAL BREEDING

AS a result of the development of artificial breeding during the last decade it is important that the principles as well as the practical procedures used in this field be made available to livestock breeders. Mr. Stamm has contributed a highly readable and well illustrated account of this expanding field.

The section of this book dealing with the breeds of livestock is an excellent condensation of the important characteristics of the various breeds. The photographs are of high quality and contribute to the usefulness of the text material. One of the outstanding features of this book is the "Directory of Semen Producers." A complete index to the book is included. The portion dealing with the principles of veterinary obstetrics is well presented for the layman because the basic facts have been included in the discussion of pregnancy and parturition. The book would have been improved if recent material dealing with the principles of genetics and the physiology of development had been included. The interesting summary dealing with "defects that animals are born with" is commendable and includes a short but adequate discussion of the dwarf problem.

In an attempt to simplify and generalize the author has introduced minor technical errors in the text which should have been avoided. For example, on page 13, the following statement appears relative to the physiologic activity of the female sex hormone in the cow: "So powerful is this estrogen that the daily requirements of a cow weigh only half as much as a postage stamp." Quantitative data from adequate experiments are lacking on this important point. On page 64 it is noted that glycerol is mentioned as a diluter rather than a constituent of an extender. Methyl alcohol should have been indicated as the fluid used in the bath for freezing semen rather than "alcohol." More care should have been used in preparation of captions as is shown in the description of the illustration on page 49. The illustrations of the sperm and egg (page 8) and of the cow's ovary (page 13) are inferior. Furthermore, the usefulness of this book would have been enhanced considerably by including a brief presentation of the anatomy and physiology of the male reproductive tract. Such fundamentals are necessary to an understanding of the composition and function of the constituents of semen.

It is the opinion of this reviewer that the author has succeeded in presenting in simple, non-technical language a useful and timely discussion of the field of artificial breeding and its problems. The Windsor Press is also to be complimented for their contribution in the production of this practical book.

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Artificial Breeding and Livestock Improvement. G. W. Stamm. Windsor Press, Chicago, 1954. 304 pp. Illus. $3.50.

FURTHER STUDIES ON A LETHAL SERIES IN THE HONEY BEE

OTTO MACKENSEN*

IT is assumed that a haplo-viable, homozygous lethal series of alleles exists in the honey bee (*Apis mellifera* L.). In a previous paper[1] data upon which this assumption is based were presented. Members of this series might be designated *a*, *b*, *c*, *d*, etc. Females (queens and workers) are always heterozygous (e.g. *a/b* or *c/d*), and queens produce two types of haploid males (drones) in equal numbers (e.g. *a* and *b*, or *c* and *d*). The homozygotes do not hatch. Although this series of alleles is similar in lethal action to the sex alleles of *Habrobracon*,[2,3] an association with sex has not been shown in the honey bee. The data presented here demonstrate 11 alleles in this series.

Materials and Methods

The general plan was to cross lines containing only two lethal alleles in all possible combinations by individual artificial matings. From the results of such crosses the relationship of the lethal alleles in all lines can be determined as follows. If the drone carries an allele different from the two alleles of the queen (e.g. $a/b \times c$), the theoretical hatchability will be 100 percent. If he carries an allele similar to one of those of the queen (e.g. $a/b \times a$), the theoretical hatchability will be 50 percent because the homozygotes do not hatch. Because of factors other than the lethal alleles being studied, hatchability seldom reaches the percentages theoretically possible. A series of individual matings between queens of one two-allele line and sons of a queen of another two-allele line will give one of the following results: If the two lines have no allele in common (e.g. *a/b* queens and *c* and *d* drones), all progenies will be highly hatchable. If the two lines have both alleles in common (e.g. $a/b \times a$ and *b* drones), all progenies will be poorly hatchable. If the two lines have only one allele in common, then one-half the progenies will be highly hatchable and the other half poorly hatchable.

Six lines from various sources were used in these experiments. Only two of the lines were related—the SW-1 and SW-3 lines. They were originated from sister queens descending from a commercial Italian stock. The B line came from English stock maintained by artificial insemination since its importation in 1947. The A-18 line was started in 1947 from a strain which had been established in 1937 from a mixture of bees from several sources and bred by natural mating through 1945 and by artificial insemination thereafter. The W-39 line was established in 1949 from an Italian stock imported from Italy in 1937 and bred first by isolated natural mating and after 1943 by artificial mating. The W-42 line was derived from Caucasian stock obtained from a commercial breeder in 1948 and maintained by artificial insemination since that time.

When once established, all two-allele lines were maintained by artificial insemination. As a further precaution against contamination the drones were reared in colonies stocked with bees of a distinguishable color, so that drones from laying worker bees could be recognized and discarded.

Two methods were used to reduce the lethal alleles in a line to only two. In one method a queen was mated to her sons and the line continued by brother-sister mating. Since a queen contains only two alleles, this procedure automatically reduces the number in the resulting line to two. This method was used only in line A-18. In the other method a series of individual brother-

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sister matings was made. In such a series of matings some two-allele families are always produced regardless of the composition of the drones to which the mother was mated. Sibling matings between sons and daughters of one of the queens producing eggs of low hatchability served to establish the two-allele line.

Hatchability tests were made as follows: When the queen laid normally, a fresh comb was added for the queen to lay in for one day, the comb checked to see that a solid area of eggs had been laid, and survival determined on the fifth day, when the youngest larvae were one day old, by counting the cells occupied by larvae of the right age in one or more 100-cell areas. The comb remained in the hive and the queen continued to lay in it. A piece of cardboard in which a rectangular hole the size of 100 cells had been cut was placed over the comb to mark the area to be counted. There was little chance of confusion in age of larvae, because most inviable eggs are not removed until hatching time, three days after deposition. When the queen laid abnormally, placing eggs in odd positions or more than one to a cell, she was permitted to lay in a fresh comb for one day, an area within the laid area was defined, and eggs were destroyed that were poorly placed or placed more than one to the cell. The remaining eggs were then counted, and the comb was placed over a queen excluder in a strong colony until the surviving larvae were counted on the fifth day. This method was used mainly on queens of line A-18, the most highly inbred line.

When individual matings are made by artificial insemination, the spermatheca sometimes receives too few sperms for all eggs to be fertilized. All progenies were therefore observed long enough to determine the sex of the individuals and eight progenies with more than an occasional drone were eliminated. These were scattered throughout the crosses.

TABLE I. Crosses and number of progenies of high or low hatchability

Lines crossed	High	Low	Not tested
SW-1 × SW-3	4	7	–
SW-3 × SW-1	9	8	–
SW-1 × B	8	–	–
B × SW-1	16	–	–
SW-1 × A-18	21	–	–
W-42 × SW-1	18	–	–
SW-1 × W-39	11	–	–
B × SW-3	15	–	–
SW-3 × A-18	10	–	–
A-18 × SW-3	–	–	4
W-42 × SW-3	13	–	3
SW-3 × W-39	13	–	–
B × A-18	16	–	–
B × W-42	8	–	–
B × W-39	16	–	–
A-18 × W-42	6	–	–
W-42 × A-18	16	–	–
A-18 × W-39	15	–	4
W-39 × W-42	12	–	–

Results and Discussion

The results of all the crosses are summarized in Table I. Hatchability was classed as low when 50 percent or under, and as high when over 50 percent. It varied with the line source and the inbreeding of the cross mated queens. High hatchability ranged from 60 to 99 percent and low hatchability from 40 to 50 percent.

Some of the queens of lines W-42 and A-18 laid so few eggs and placed them so poorly that a reliable hatchability test could not be made. The progenies mothered by these queens were relatively few in number and occurred only in crosses in which all the reliable tests were high. They are listed as "not tested" in Table I. Although in the A-18 × SW-3 cross all four queens laid too poorly to test, all 10 progenies of the reciprocal cross, mothered by excellent layers, tested high. Reciprocal crosses to the A-18 × W-39 and W-42 × SW-3 crosses are not available.

Only one combination of lines, SW-1 × SW-3, and the reciprocal cross produced progenies approximately half low and half high in hatchability, indicating that these lines had an allele in common. All the other combinations produced only highly hatchable progenies, indicating non-identity of lethal alleles. It is concluded that 11 different alleles are represented in the six lines tested, since the maximum possible number is 12. This number is not surprising, when it is considered that most of the lines come from unrelated sources. With this number in only six lines, there must be many more in the bee population of the world.

Summary

Six inbred lines of the honey bee (*Apis mellifera* L.), each containing only two alleles of a series of haplo-viable homozygous lethals, were crossed in all possible combinations by individual matings. By a study of the ratio of high- to low-hatchability progenies of each cross it was determined that 11 alleles were present.

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VITAL FACTORS IN HUMAN LIFE

THE comparative twin data presented in this German monograph* cover a period of 25 years—or a fraction of this time if observation was ended by death before the end of the given period—in the histories of 50 (22 ♂♂, 28 ♀♀) two-egg and 100 (44 ♂♂, 56 ♀♀) one-egg twin pairs. Equally impressive is the length of time, during which the author has been active as a pioneer in the use of the twin study method, generally keeping his research in line with his training, that is, on the physical side of human personality development. Like Francis Galton, the first systematic twin researcher at the dawn of modern human genetics, he favors longitudinal over cross-sectional investigations, without going to extremes in his preference. In other words, no claim is made that either approach can actually replace the other, even if longitudinal studies are understood to call for continuity of observation as an essential requirement. In the author's study, the mean age of the twin subjects was 16 years at the time of the first examination (1924), 18½ years at the time of the first control examination (1926-1927), and 40 years at the time of the final examination (1950), thus raising certain doubts as to both the representativeness and continuousness of the series studied. With respect to physical characteristics, a distinction is made between stable ("umweltstabile") and unstable ("umweltlabile") types of genetically determined traits. Height and head length are referred to as the prototypes of the former group of traits, and body weight as that of the latter. The scope of this analysis is complicated by a division of environmental constellations into "concordant" and "discordant" ones. By and large, however, the anthropometric data compiled are interpreted in the sense of "a remarkable constancy of the body type developed." In contradistinction to two-egg pairs, one-egg twins are said to be distinguished by the tendency to become more similar as they grow older, both physically and mentally.

Some observed intra-pair personality differences in response to dissimiliar life experiences are used in an attempt to differentiate people according to the degree of their behavioral variability. For this purpose, a highly resistive or non-variable medium group is contrasted with two relatively changeable groups at the opposite extremes of the scale, an intellectually inferior ("primitive") group rendered susceptible to environmental influences by its lack of inner resources and an intellectually superior group capable of adaptation to different environments through selective development of one or another of a great variety of personality potentials. The usefulness of the three classifications is reduced by the fact that they seem to have been derived without the benefit of adequate psychometric procedures.

The observation of a possibly excessive number of one-egg pairs with childlessness of one member is ascribed to disturbances in the sexual development of female twins. Once again, this conclusion appears hypothetical and supported only by rather generalized impressions. The sections dealing with intensified sibling rivalry in twins and an analysis of milieu-conditioned personality changes tend to be on the vague side, too.

Even more mystifying is the author's concept of a "third force" affecting human life. The concept is introduced in order to explain the occurrence of certain diseases showing "no causal relationship either to heredity or to environment" (nor a difference in discordance between one-egg and two-egg twins). The pathological conditions classified in this manner are divided into (1) "microphysical"

**Wirksame Faktoren im Leben des Menschen* (Beobachtungen an ein-und zweieiigen Zwillingen durch 25 Jahre), by Otmar Frhr. Von Verschuer (Director, Institute of Human Genetics, University of Muenster), Wiesbaden, F. Steiner, 1954. Pp. 288.

phenomena convertible into processes of macrophysical significance, (2) certain virus infections, and (3) psychosomatic disorders. The relative frequency of these conditions is viewed as a deplorable limitation to an analysis of twin histories in terms of genetic and environmental influences. In consequence, disease and death are thought of by the author "as events in human life which frequently defy prediction."

The rather unexpected failure of the 13 one-egg pairs in this German study to reveal smaller intra-pair life span differences than the five two-egg pairs of the series would seem to be explainable without resorting to the "third force" theory of the author, that is, without minimizing the available evidence in support of the thesis that gene-specific health potentials and survival values are the basic determinants of the human life span. Although the observed mean intra-pair differences in the two same-sex groups were 5.6 and 4.5 years, respectively, this somewhat disconcerting reversal in mean life expectancies may indicate only that life in Germany during Hitler's regime was as unsafe for twins as it was for single-born persons. In fact, in no less than 13 of a total of 15 male pairs compared with respect to their life spans, either one or both twin partners (four and nine pairs, respectively) were killed in action or ended by suicide. With a violent death risk of nearly 75 percent for middle-aged men, however, it would probably be difficult for any group of males to take sufficient advantage of optimum longevity potentials.

In spite of these weak points in the author's data and in some of the conclusions derived from them, the book is interesting to read and always thought-provoking. It is well-printed and richly documented, and it certainly demonstrates not only the unique potentialities of longitudinal twin studies based on statistically representative samples, but also the stupendous difficulties which may be encountered before such a study is successfully completed.

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DR. MULLER DISCUSSES THE RADIATION HAZARD

Speaking before the National Academy of Sciences on the occasion of the Kimber Genetic Awards ceremonies, Dr. Muller took occasion to discuss the very live question of radiation hazards, due not only to atomic tests but to careless uses of X-ray in medicine and industry.

RECENT denials of damaging hereditary effects by atomic radiation "weaken public morale and open the door for defeatist propaganda," it was charged here Monday night by Indiana University's Prof. H. J. Muller, Nobel Prize winning geneticist.

"So many people are already aware of the damaging action of radiation on heredity," he said, "that these attempts in high places to disclaim the danger cause the public to lose confidence. On the recoil, the public then becomes more likely to swallow another widely circulated counterclaim that the hereditary constitution of all of humanity is being seriously undermined by our tests of hydrogen bombs and that the tests should be stopped for this reason.

"In my view," Muller said, "this claim is equally false, and is being put out in a manner that leads me to infer that, behind the scenes and unknown to the many who advocate it sincerely, it is being instigated by the Communists."

Muller is one of the world's leading authorities on the genetic effects of radiations. He won the Nobel Prize in medicine in 1946 for proving that X-rays produce mutations, or changes in the genes, the heredity controlling factors in reproductive cells.

Muller disputed recent claims that radiation, even in such quantity as that to which the people of Hiroshima were exposed by the atomic bomb, would cause no damage to later generations. "The group of responsible scientists," he said, "who in 1953 signed the official report on investigations of the Hiroshima-Nagasaki after-effects, stated that it had 'always been doubtful whether significant findings' could be obtained by the methods there used. They pointed out that the inconclusive results, while not definitely positive, were at the same time 'entirely consistent with what is known of the radiation genetics of a wide variety of other material.'

"In other words," Muller said, "there could well have been as many harmful mutations produced in these human populations, but lying undetected, as experiments with other animals have shown to be produced in them by such exposure.

"The numerous disabilities and deaths among Hiroshima survivors will be spread out very thin over a large number of generations," Muller asserted. "The effect in any one individual usually will be slight, although enough finally to extinguish his line of descent. Therefore, the overall cost, although great, will be

too scattered and insidious to affect the population as a whole noticeably."

Muller attacked recent assertions that heavy exposures of human beings to radiation may even result in their descendants being benefitted. "This sort of thing," he said, "has been found to occur in fruit flies irradiated heavily for generations because, in fruit flies, it is the usual thing for more than 100 young to die for every one that survives. Thus the many flies inheriting a weakened heredity tend to die out fairly quickly.

"They could be replaced by the rapid multiplication of the extremely rare beneficial mutations that were produced. But in a human population such a situation would be ruinous."

Referring to the H-bomb tests in the Pacific, Muller said, "The Atomic Energy Commission has recently stated that the radiation received by the average American from these tests to date is only about as much as is received from a chest x-ray, or one-tenth of an r-unit. Since there were 160 million people receiving this H-bomb radiation, as compared to the 160,000 persons who survived Hiroshima after getting a thousand times this dose, there must have been about as many mutations in both areas."

Muller cited figures showing that this amount of radiation could lead to tens of thousands of harmful mutations inherited by the next generation. "However, relatively to the size of the two populations," he said, "the effect is only a thousandth as great in the U.S.A. as a whole as was concentrated in Hiroshima. This certainly does not undermine the heredity of our population as a whole significantly.

"Each individual harmful mutation is, however, an evil, and we have no right to dismiss it lightly. Therefore we must base our case for the continuance of the tests squarely on the fact that they are at the present stage necessary to prevent our being put at a military disadvantage. Only from a position of all around strength, I think, can we finally reach a situation where general disarmament is feasible.

"The same kind of reasoning," Muller said, "justifies the use of carefully controlled X-rays and radioactivity in medicine. That is, the genetic damage should be admitted and weighed against the benefits. But a recent survey shows that Americans are receiving much more radiation in these ways than as a result of all atomic and hydrogen test explosions.

"Most of the genetic damage from medical uses of radiation could be avoided if only physicians would admit its existence and take certain simple precautions to reduce it, such as shielding the reproductive organs, and limiting and keeping track of the total amount of exposure of each patient over many years.

"It is largely this reckless attitude on the part of physicians which has influenced extremists to claim that nuclear explosions are harmless or even beneficial."

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Here's an opportunity to own Francis Galton's famous statistical study of HEREDITY GENIUS. In this monumental work, Galton analyzes the family tree of several hundred statesmen, military leaders, poets, scientists, athletes, musicians and judges to find out whether the transmission of mental faculties from generation to generation follows Mendelian principles. First published more than 60 years ago, it is the book that . . .

ATAXIA — A NEW RECESSIVE MUTANT OF THE HOUSE MOUSE

MARY F. LYON*

THE name ataxia, symbol *ax*, has been given to a new autosomal recessive mutant of *Mus musculus*, affecting the locomotory system. The mutation occurred spontaneously in the CBA inbred strain, among animals in the control series of an experiment involving the induction of mutations by gamma rays.[2]

Description

The main defect of ataxic animals is a progressive paralysis of all four limbs, which first appears in the third week of life and becomes progressively worse until two or three months of age.

In routine observations ataxia could not be classified with certainty until after 18 days of age. By special daily examination of young mice from birth, however, abnormalities were detected at about one week of age. At this stage animals later classified as ataxic were more active than their normal sibs, and also seemed to hold the legs unduly straight when walking. The normal week-old mouse crawls with the belly resting on the ground, but ataxics ran rapidly with the body lifted clear of the ground. Some animals showed a tremor of head and body and some an occasional disturbance of the normal diagonal sequence of limb movement. This type of behavior continued until the age of about two weeks, when the hyperactivity seemed to be lost. Some ataxics, but not all, could then be distinguished by a tremor of head and body.

The next stage was the development, during the third week of life, of a "stiff" gait. The animals could run at a fairly normal speed but the steps were shorter than usual, giving a stiff, shuffling appearance. From this time there was a steady increase in paralysis up to two or three months of age.

Three apparently distinct features of the paralysis were (a) tremor, (b) loss of coordination of limbs, (c) weakness of limbs. The tremor affected head, body and limbs. A characteristic feature was a rapid beating movement of the forelimbs when the mouse was held up by the tail. If this tremor was not already present by three weeks of age it appeared within the next two or three weeks. Weakness of the limbs developed in parallel with the loss of coordination, so that the abilities of both balance and propulsion were lost at the same time. At three weeks the normal diagonal sequence of movement of the limbs was usually still present. Later, however, the animal began to move the hind-limbs together instead of in sequence, and to leave them in the retracted position for too long. Figure 9*A* shows such a mouse, which has brought both hind-limbs into an abnormal retracted position and has remained like that for a minute or so. By about five or six weeks the ability to sit up on the haunches was lost; the gait became progressively slower, and overbalancing of the hindquarters began to occur. In the end a state was reached where the animals could not remain in the normal prone position at all, but lay on one side and could only drag themselves along very slowly with the forelimbs (Figure 9*B*). There was no further deterioration after three months of age and the neuro-muscular condition did not in itself seem to cause death. The tail and fur of the abdomen tended to become wet with urine and faeces, however, leading to skin irritation, and when this happened death usually occurred shortly thereafter.

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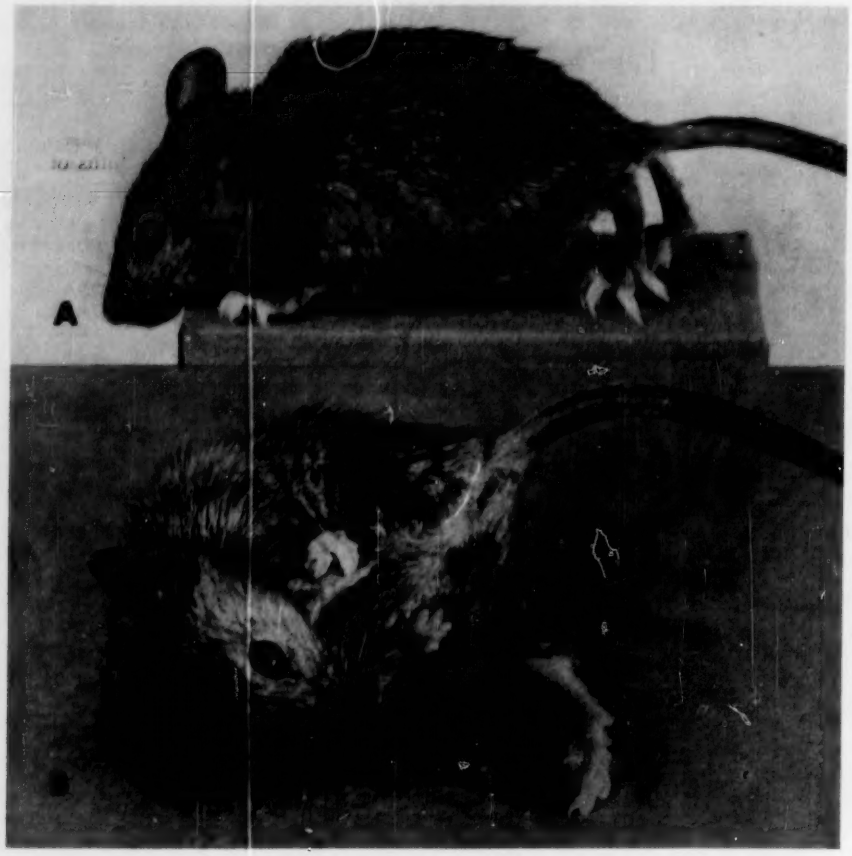

THE ATAXIC MUTUANT

Figure 9

A—Ataxic mouse showing the abnormal retracted position of both hind limbs. *B*—Ataxic mouse which can no longer balance in the prone position and is trying ineffectively to propel itself while lying on its side.

Ataxic mice always remained much smaller than their normal sibs. Some slowing of growth was present from birth; at one week ataxics weighed 10 percent less than their normal sibs and by three weeks the difference had increased to 25 percent. From then on growth was very slow and by five or six weeks affected animals were only half the normal weight.

All ataxics paired with normal mice proved sterile, and on dissection the gonads were small and the accessory sex organs immature.

Segregation and Linkage Relations

In the hope of finding a close linkage which would ease the difficulties of maintaining the gene, animals which had borne ataxic young were outcrossed to the five linkage-testing stocks of Carter and Falconer.[1] The outcross progeny were then tested for their ability to produce ataxics; those which did were then mated together to give data on the single fac-

tor segregation and linkage relations of the mutant.

Single Factor Segregation. From these linkage-testing intercrosses for ataxia 1516 animals were raised, 1181 normal and 335 ataxics. The observed frequency of ataxia is thus 22.1 percent and there is a significant departure ($\chi^2 = 6.81$, $P<.01$) from the 3:1 ratio expected on the hypothesis that *ax* is a simple recessive gene. Despite the significance of the discrepancy, however, it is sufficiently small to be explained by differential mortality or incomplete penetrance of *axax*, the former being the more probable. The proportion of tested progeny of heterozygotes which were themselves heterozygous gives further information on the segregation of *ax*. When a heterozygote is mated to a homozygous wild-type animal a 1:1 ratio of $+ax$ to $++$ progeny is expected; and when a heterozygote is mated to another heterozygote a 2:1 ratio is expected, among the non-ataxic progeny. It is necessary, however, to correct for the fact that an animal is not conclusively proved $++^{ax}$ by the non-appearance of ataxics in its progeny. If only a few young are obtained there may be an appreciable probability that the animal under test is, in fact, $+ax$, but has failed by chance to produce any homozygotes. To allow for this, Falconer[5] developed the concept of "completeness of test." In this instance, the frequency of ataxics observed in known intercrosses is 22.1 percent; then each animal tested with n progeny by a known heterozygous mate is equivalent to $[1-(1-0.221)^n]$ completely tested individuals. If the number of $+ax$ heterozygotes found is then deducted from the "equivalent completely tested total," the remainder gives the equivalent number of $++^{ax}$ animals among the sample. When this correction is applied the results show good agreement with expectation, and fully support the hypothesis of a simple recessive gene (Table 1).

TABLE I. Segregation of normal progeny of $+ax$ animals

Progeny tested	Mating type of parents $+ax \times ++$	$+ax \times +ax$
Total number	218	63
Completely tested equivalent	*166.7*	*47.3*
$+ax$ heterozygotes found	80	31
$+ax$ heterozygotes expected	*83.35*	*31.53*
$++$ homozygotes, by subtraction	86.7	16.3
$++$ homozygotes, expected	*83.35*	*15.77*

Linkage. The segregation of *ax* with 20 linkage group markers and sex is shown in Table II. In only one test was any suggestion of linkage obtained. Repulsion intercrosses between *ax* and the albino alleles, *c* and c^e, indicated 39.9 percent recombinaiton, with a linkage chi-square of 6.1. However, coupling tests which were then made up indicated 51.8 percent recombination with a chi-square of only 0.09, and so failed to confirm the indication of a linkage. The linkage group to which *ax* belongs thus remains unknown.

Comparison with Other Mutants

The locomotory defects in ataxic animals do not closely resemble those described for any other mouse mutant. There is a general resemblance, however, to wobbly, *wb*,[6] jittery, *ji*,[3] and wabbler-lethal, *Wl*.[4] The non-allelism of *ax* with *wb* was proved by mating $+ax$ heterozygotes to $+wb$ heterozygotes. All of

TABLE II. Linkage tests with *ax*

(A) *Recessive mutants: matings of double intercross type*

Mutant	Phase[a]	++	+*ax*	m+	*max*	Total	Recombination %	χ^2
a	R	64	23	24	8	119	48.9 ± 6.9	0.025
b	R	50	19	15	4	88	45.5 ± 8.0	0.122
c, c^e	R	188	74	64	10	336	39.9 ± 4.1	6.108
c, c^e	C	96	31	29	8	164	51.8 ± 5.9	0.096
f	R	133	46	16	10	205	45.5 ± 5.2	0.718
fu	R	138	53	41	12	224	52.7 ± 5.0	0.282
ja	R	115	44	35	13	207	49.4 ± 5.2	0.013
In	R	206	40	60	17	323	54.6 ± 4.2	1.205
p	R	132	31	42	13	218	51.5 ± 5.1	0.463
ru	R	109	42	41	15	207	49.4 ± 5.2	0.014
s	R	210	49	57	7	323	46.5 ± 4.2	0.697
se	R	79	19	21	5	124	50.8 ± 6.7	0.015
sr	R	80	22	18	1	121	47.4 ± 6.8	0.149
tes-2	R	213	42	54	14	323	54.0 ± 4.2	0.897

(B) *Dominant mutants: matings intercrosses for ax and backcrosses for marker*

Mutant	Phase[a]	*M+*	*Max*	++	+*ax*	Total	Recombination %	χ^2
Ia	C	22	7	72	16	117	59.8 ± 8.0	1.501
N	C	93	42	131	37	303	58.7 ± 5.0	3.084
Ra	C	77	21	64	17	179	49.7 ± 6.5	0.002
Sd	C	50	13	53	11	127	53.5 ± 7.7	0.213
T	C	105	26	91	36	258	41.5 ± 5.4	2.496
Va	C	69	15	75	27	186	41.9 ± 6.4	1.613
Mi^{wh}	C	69	19	80	27	195	46.7 ± 6.2	0.291
♂	C	100	32	77	34	243	44.0 ± 5.6	1.162
♂	R	77	24	84	22	207	46.8 ± 6.0	0.274

[a] C = coupling; R = repulsion.

Falconer[5] developed the concept of "completeness of test." In this instance, the frequency of ataxics observed in known intercrosses is 22.1 percent; then each animal tested with n progeny by a known heterozygous mate is equivalent to $[1-(1-0.221)^n]$ completely tested individuals. If the number of $+ax$ heterozygotes found is then deducted from the "equivalent completely tested total," the remainder gives the equivalent number of $++^{ax}$ animals among the sample. When this correction is applied the results show good agreement with expectation, and fully support the hypothesis of a simple recessive gene (Table 1).

Linkage. The segregation of *ax* with 20 linkage group markers and sex is shown in Table II. In only one test was any suggestion of linkage obtained. Repulsion intercrosses between *ax* and the albino alleles, *c* and c^e, indicated 39.9 percent recombinaiton, with a linkage chi-square of 6.1. However, coupling tests which were then made up indicated 51.8 percent recombination with a chi-square of only 0.09, and so failed to confirm the indication of a linkage. The linkage group to which *ax* belongs thus remains unknown.

Comparison with Other Mutants

The locomotory defects in ataxic animals do not closely resemble those described for any other mouse mutant. There is a general resemblance, however, to wobbly, *wb*,[6] jittery, *ji*,[3] and wabbler-lethal, *Wl*.[4] The non-allelism of *ax* with *wb* was proved by mating $+ax$ heterozygotes to $+wb$ heterozygotes. All of

19 young were normal. Jittery shows close linkage with waltzer, *v*,[7] and ataxia shows no such linkage, so these two again are not allelic. No tests with wabbler-lethal have been made, but this mutant is clearly not identical with *ax* as it is lethal at three or four weeks.

No histological studies of ataxic animals have been made.

Summary

Ataxia, *ax*, is a recessive mutant affecting locomotion. In the third week of life a progressive paralysis appears, with tremor, loss of coordination and limb weakness. This leads to almost complete helplessness by three months of age. Homozygotes are sterile. There is a slight but significant shortage of ataxics in the progeny of intercrosses, probably due to increased mortality. Extensive linkage tests have failed to show the linkage group to which *ax* belongs.

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KIMBER GENETICS AWARDS TO WILLIAM E. CASTLE AND HERMANN J. MULLER

THE Kimber Genetics Award, presented for the first time this year, has been established by the Kimber Farms Foundation of Niles, California, to recognize distinguished scientific contributions in the field of genetics, either through single accomplishments of unusual significance or through a long period of significant productivity. Two awards were made: to William E. Castle, Emeritus Professor of Genetics at Harvard University and now Research Consultant to the University of California, and to Hermann J. Muller, Professor of Zoology at Indiana University. Both men are members of the Academy.

Dr. Castle, who is 87, is regarded as the founder of mammalian genetics in the United States. Near the turn of the century his research showed decisively the role of what we now know as genes as the mechanisms by which inherited characteristics are transmitted. His long career has been unusually fruitful, both as a teacher of the leading mammalian geneticists in the United States today and as a contributor to the science of genetics. Dr. Castle was presented the award, *in absentia*.

Among Dr. Muller's most important contributions to genetics have been his studies of the genetic effects of radiations. This work has shed much light on the structure and function of the chromosomes. Dr. Muller was awarded the Nobel Prize in Physiology and Medicine in 1946 in recognition of his outstanding work.

The award is made by the National Academy of Sciences upon recommendation of a selection committee that includes three members named by the Academy, one named by the Genetics Society of America, and one named by the American Association for the Advancement of Science.

THE FIRST INTERSPECIFIC WHEAT HYBRIDS

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IT is not generally known that the first interspecific wheat hybrid experiments were performed and reported about one and one-half centuries ago (1807) by Carlo Antonio Ludovico Bellardi (1741-1826) who was assistant professor of agriculture at the University of Pavia, and later professor at the University of Turin. He was a pupil of Allioni and collaborated with him in the preparation of the "Flora Pedemontana." One of the earliest of many papers on botanical subjects was a study on the sensibility of the mimosae (*De Mimosa Sentiente,* 1764). The genera *Bellardia* Colla and *Bellardia* All. were named for him. Two biographies have been published.[3, 4].

Bellardi's collaborator on the wheat experiments was the taxonomist, Giuseppe Bayle Barelle (1768-1811). Barelle was a professor of agriculture at the University of Pavia where he founded the agricultural garden, now a geophysical observatory. In addition to two text books, he wrote an agronomic monograph on cereals. However, only the first part (wheat) has been published.[1] A sketch of his life has been compiled by E. Beltrami.[3]

The results of the experiments of both men were published in the *Annali Dell' Agricultura Del Regno D'Italia* in 1809. The founder and editor of this journal was the famous agronomist Conte Filippo Re, who was one of the first monographers of plant diseases.[8]

Bellardi's paper is divided into 19 short chapters, and enriched with a fine copper engraving (reproduced here as Figure 10). Since the periodical[8] in which the paper appears is not readily available for reference, this author has briefly summarized the chapters below.

1. Brief introduction on plant sexuality with reference to Haartmann's paper on hybrids.* Reference is also made to papers published on the same subject in Russia during the years 1782 and 1786.

2. Reference to the dioecious species (date palm and hemp, but corn is also considered) and the interrelationship between rainfall and pollinization.

3. It is stated that, in the beginning, very few vegetables were present in Nature. Many new species were then 'created' by "spurious hybridization," but probably not all the possible combinations were yet developed. Apparently, this is the first clear-cut affirmation on the origin of new, cultivated species by interspecific hybridization.

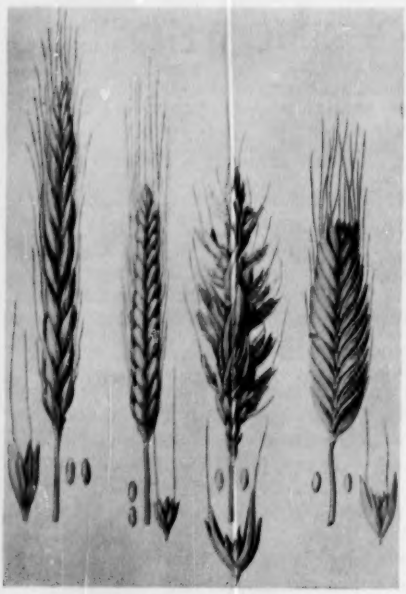
4. Fecundity of interspecific hybrids in animals and plants. It is shown that an improvement in animals is obtained through intraspecific crossing. Examples are furnished.

5. Morpho-anatomical analogies between the plants are favorable both to intra- and interspecific crossing, and possibly to intergenetic hybridization.

6. The origin of naked barley is attributed to the cross of common barley ♂ × wheat ♀, since the spike is that of a barley, but the caryopsis is that of wheat.

7. It is proposed to select mother plants according to the characteristic to be improved, e.g.: The covered wheat with brittle axis and the grain rich in protein with the common, naked wheat having tough axis. According to the reference in the Bayle Barelle mono-

**Plantae Hybridae quas sub praesidio D. D. Caroli Linnei Pubblicae Disquisitioni sistit* Joannes Luis Haartmann Austro-Finlandus. This paper has not been quoted by Pritzel (*Thesaurus Literaturae Botanicae* [Brockhaus] (Lipsiae, 1872) under this title, but it is certainly *Plantae Hybridae* (Upsaliae, 1751), an academic thesis presented by Linné. J. J. Haartmann was the Editor of the Swedish edition of *Linnaeus' Systema Naturae* (Stockholm, 1733).



EARLY WHEAT HYBRIDS
Figure 10

Four varieties are shown from left to right as follows: *Triticum polonicum*; *T. tomentoso-polonicum*; *T. polonico-compositum* and *T. polonico-coeruleum*.

graph, the first species is the large spelt, *Triticum spelta*. (It should be noted that the example is selected among hexaploid wheats).

8. Possibility of improving adaption to different environments by plant hybridization.

9. Professor Bayle Barelle made the first cross (April 1806) *T. polonicum* ♀ × *T. compositum* ♂ in the agricultural garden of Pavia, obtaining fertile grains.[1] The subsequent year the author made the crosses *T. coerulescens* ♂ × *T. polonicum* ♀ and *T. tomentosum* ♀ × *T. polonicum* ♂. (In agreement with the current taxonomy of the genus *Triticum*, it is possible to recognize the species—and up to a certain point the varieties—of wheats described by Bayle Barelle and Bellardi as follows:

T. polonicum.—A long awned form, with squared, lax ear; bearded spikelets; hairy glumes; long, not very narrow grain; color of the glumes and grains not stated. Bellardi[2] quoted Bayle Barelle fully. According to the latter, this form of *T. polonicum* is that of a long-awned wheat, with foliaceous, white glumes, oblong grain, long and narrow, 'fair' perlaceous grain. Color and hairyness of glumes not stated. It is not possible to recognize the botanical variety; if the glumes were smooth it may be the Mediterranean var. *levissimum* Hall., or, if the glumes were hairy, the var. *villosum* Desv. another Mediterranean variety, in past centuries more diffused in Italy than the first one. Probably it was the var. *levissimum*, since the hairyness of the glumes is indicated as a differential characteristic of the third hybrid (see below) as related to the mother species *T. polonicum*.

T. compositum L. is the *Frumentum racemosum* of Anguillara, namely the 'Bled de Miracle' of the old French language, known under many common names in the Italian language, the commonest one being 'Grano Mazzocchio' (old) or 'Grano del Miracolo' (comparatively new). The outstanding characteristic is the branched spikelet, recognized as a varietal or subvarietal genus by Flaksberger,[6, 7] and now known as a species (verbal communication of Jakubtziner). The plant is described as having white-yellowish grains, short awns, solid stem, hairy glumes. Bellardi referred to this species, according to Desfontaines, as *T. durum*. Unfortunately the color of the glumes has not been indicated, so that it may be the var. *valenciae* koern., *fastuosum* Lagasca, *italicum* Alef., or *aegyptiacum* Koern. According to Flaksberger[6] it is the var. *italicum*, and we agree with this opinion, as this variety was one of the most diffused in the old cultures of Lombardy, up to the first half of the past century.

T. coerulescens is a hard wheat cultivated in Sicily, and probably the same wheat called *T. coeruleum* by Arduini. It possesses long awned glumes with a bluish or bluish-violet coat, and dull, fair, alabastrine grains. It has been generally recognized as a variety of

T. durum, cultivated in the Mediterranean belt of *durum* wheats, but has now apparently disappeared from Italy.

The *T. tomentosum* Bayle Barelle ('Grano Ravanese' of Tuscany) is a black-awned variety, superficially described but clearly illustrated by this student. It is different in some respects but also resembles *T. turgidum*. This wheat is commonly attributed to the var. *italicum* Alef., formerly of common culture in the Mediterranean countries, but now rare in southern Italy. According to Flaksberger[6] it is the form *tomentosum* of this variety.

10. In the month of June of the year 1807, the author observed the fruit yield of Bayle Barelle's hybrid, and noted characteristics different from the previously known varieties. This was proved by the crosses made by the author himself.

11. A short discussion on the nomenclature of the hybrids. In conclusion the word *hybridum* is to be used when the parents are unknown, but not when the mother plant is known.

12. Because the similarity of the hybrids obtained with *T. polonicum*, the word *polonicum* must be prefixed to the binomial, specific name. The author proved the 'constancy' of Bayle Barelle's hybrid in the first year of culture (1808).

13.-15. In conclusion, the following binomial-composed nomenclature has been established:

× *T. polonico-compositum* (= *T. polinicum* var. ? × *T. durum* var. *italicum*);

× *T. polonico-coeruleum* (= *T. polonicum* var. ? × *T. durum* var. *coerulescens*);

× *T. tomentoso-polonicum* = *T. durum* var. ? *italicum* f. *tomentosum* × *T. polonicum* var. ?).

The hybrids are fully described in both Latin and Italian, and the difference with *T. polonicum* underlined in both languages.

(It must be noted that Bellardi's *T. polonico-compositum* has been called *T. polonicum hybridum horti ticinensis* by Bayle Barelle and probably the priority is in favor of the last polynomial. On the subject see the discussion on the use of the word *hybridum* in Chapter 9).

17. The possibility of future hybridization work is emphasized, and the technique of crossing is briefly discussed.

18. According to the observations made by the author on naked and common barleys and a few other horticultural plants, hybrid forms have a tendency to a re-hybridization, with consequent 'degeneration' up to the parent species having the greater tendency toward 'wildness'.

19. Conclusion and general summary.

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FURTHER STUDIES OF LINKAGE IN THE THIRD CHROMOSOME OF THE RAT

W. E. CASTLE*

EARLIER studies have shown that three recesive genes lie in a common linkage system in the third chromosome of the rat. These are genes for two different forms of hairlessness, called naked (*n*) and hairless (*hr*), and a gene for wobbly locomotion (*wo*). It has been shown that *n* and *hr* are linked with each other, the observed crossover percentage being 34.7 ± 4.8. It has also been shown that *hr* and *wo* are linked with each other, the observed crossover percentage being 40.3 ± 3.1. But no indication was found of linkage between *n* and *wo*, the observed crossover percentage being 51.7 ± 3.6. The conclusion was drawn that the order of the genes is *n* — *hr* — *wo* and that the end genes of the trio are so far apart that they show practical independence in transmission.

To get a more exact knowledge of the relations of the three genes, the following experiment was made.

A three point cross was made in which genes *n* and *wo* were introduced from one parent and *hr* from the other. A triply heterozygous male of constitution $\frac{n \quad wo}{\quad hr}$ was then outcrossed to normal females and the resulting young were tested individually in backcrosses to ascertain which (if any) of the three genes they carried. Eight different genotypes resulted which fall into four groups as follows:

(1) Genotypes *n-wo* and *hr* are non-crossovers;
(2) Genotypes *n-hr* and *wo* result from a crossover between genes *n* and *hr* in what will be called region 1 of the chromosome;
(3) Genotypes *n* and *hr-wo* result from a crossover between genes *hr* and *wo* in what will be called region 2 of the chromosome;
(4) Genotypes *n-hr-wo* and + + + result from crossing-over simultaneously in regions 1 and 2. They are double crossovers.

The results of these backcrosses are shown in Table I, Series A.

A second outcross (series B, Table I) was made in which the triply heterozygous male parent was of genetic constitution $\frac{wo}{n \quad hr}$. The four groups of genotypes resulting in this case were quite different; viz:

(1) Genotypes *wo* and *n-hr*, non-crossovers;
(2) Genotypes *n-wo* and *hr*, crossovers in region 1;
(3) Genotypes *n-hr-wo* and + + +, crossovers in region 2;
(4) Genotypes *n* and *hr-wo*, double crossovers.

Great care was taken to tabulate separately the results of tests in Series A and B, as otherwise they would be of no value.

The number of tested individuals in Series A was exactly 100; in Series B, it was 72; and in the two series combined, it was 172.

From the data in Table I, it was hoped that an improved estimate might be obtained of the crossover percentage between genes *n* and *hr* (region 1), and between *hr* and *wo* (region 2), as well as between the end genes, *n* and *wo*, all of which had already been tested in two-point crosses. To what extent these

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hopes have failed to be realized is shown in Table II. All of the calculated percentages lack statistical significance. Without the information supplied by earlier two-point crosses the conclusion would have been reached that the three genes are independent.

The method followed in calculating the values shown in Table II will be clear, if we follow the process through for the totals in the combined A and B series.

In region 1, the total number of crossovers observed is 47 (single) + 36 (double) = 83, which is 48.2 percent of the total 172.

In region 2 the total number of crossovers is 45 (single) + 36 (double) = 81, which is 47.1 percent of the total.

For the end genes the observed crossovers are 47 (single) + 45 (single) = 92, or 53.6 percent of the total.

In Table II, region 1, all percentages are below 50, as would be expected if genes *n* and *hr* are linked, but the deviation from 50 is in no case of significant magnitude.

In region 2 the percentages are below 50 in the A series and in the A + B total, though not in the smaller B series, but again the deviations from 50 are devoid of statistical significance.

Table II shows that, as regards the end genes *n* and *wo*, which are separated by the combined lengths of regions 1 and 2, the calculated crossover percentage is in every case in excess of 50. This is a deviation *contrary* to that expected in a case of linkage, and if it were of significant magnitude, would indicate repulsion rather than linkage.

In view of the uncertainty as to the significance of the values given in Table II, it seemed desirable to assemble all available data on the linkage relations between the three genes under study. This has been done in Table III, where the results of two-point and three-point crosses are combined.

TABLE I. Distribution of tested individuals as regards crossovers

Series	Non X	Single X, Region 1	Single X, Region 2	Double X	Total
A	28	28	23	21	100
B	16	19	22	15	72
A & B	44	47	45	36	172

TABLE II. Crossover percentages, based on Table I for gene pairs named

Series	*n*—*hr* (region 1)	*hr*—*wo* (region 2)	*n*—*wo* (end genes)
A	49.0 ± 3.4	44.0 ± 3.4	51.0 ± 3.4
B	47.2 ± 4.0	51.4 ± 4.0	56.9 ± 4.0
A & B	48.2 ± 2.6	47.1 ± 2.6	53.6 ± 2.6

In Table III there is a clear demonstration of linkage in region 2 between genes *hr* and *wo*, since the deviation from 50 percent is 3.3 times the P.E. The case is at first glance less clear in regard to region 1. Here dev./P.E. is only 2.0. The reason for its low value is the relatively small contribution of the two-point cross to the total. The two-point cross had been discontinued early when it was found that non-crossovers were regularly nearly twice as numerous as crossovers. In the case of region 2, the quantitative contribution of the two-point data to the combined total is greater, and so the demonstration of linkage is clearer in the total.

In relation to the end genes *n* and *wo*, Table III shows crossovers in excess of non-crossovers in both two-point and three-point crosses, and so in the combination total, but in no case does the excess have statistical significance. It may, however, be more than accidental.

Discussion

It would appear that the portion of chromosome 3 lying between genes *n* and *wo* is so long, or of such constitution in other respects, that the commonest event in spermatogenesis is breaking of the gene string into two or less often into three pieces.

Breaks occur in about three out of four cases, in all but 44 of the 172 tested. Single breaks occur oftener than double ones because of *interference*. The experimental data show a total of 164 chromosome breaks, of which 92 occur as singles, 72 as doubles.

Double breaks are expected to occur with a frequency equal to the product of the single break frequencies in regions 1 and 2 respectively, i.e. 45.2 × 43.3 = 19.6 percent. They actually occur with a frequency of 20.9 percent, which is only slightly greater than expectation.

Summary

Three-point crosses were made involving the recessive genes *n*, *hr* and *wo*, known from previous two-point crosses to lie in a common linkage system.

Triply heterozygous males were outcrossed to normal females, and the progeny were tested individually to ascertain which (if any) of the three recessive genes they carried.

TABLE III. Combined data from two-point and three-point crosses for gene pairs named

	n—*hr* (region 1)		*hr*—*wo* (region 2)		*n*—*wo* (end genes)	
	X	Non	X	Non	X	Non
2-point data						
3-point data	17	32	43	71	45	42
Totals	83	89	81	91	92	80
Crossover	100	121	124	162	137	122
Percentage	45.2 ± 2.1		43.3 ± 2.0		52.9 ± 2.1	
Dev./P.E.	2.0		3.3		1.3	

The results gave no clear demonstration of linkage such as had been given by the two-point crosses. But a combination of the data from both two-point and three-point crosses did establish the correctness of the assumption that the thre genes lie in a common linkage system.

The observed crossing-over between the end genes, *n* and *hr*, exceeded 50 percent in both two-point and three-point crosses, though not with statistical significance.

This suggests the possibility that when three genes lie in a common chromosome separated, each from the next, by a fairly long interval, the end genes may show *no linkage* with each other, or many even show *spurious repulsion*.

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STATISTICAL VS. DEVELOPMENTAL GENETICS

THE President of the Eighth International Congress was Dr. R. Goldschmidt, now somewhat over 80, and almost the last man who can be said to have taken part in the whole modern development of genetics since the rediscovery of Mendel's work in the first years of the century. As the theme of his opening address he took the opposition, which he suggested was in practice almost irreconcilable, between two contrasting attitudes towards genetical problems. On the one hand there is a line of approach which he called "statistical," which, when faced with a difficulty seeks to solve it by postulating new abstract genetical entities (new genes, new linkage relations, etc.) from which the observed behavior can be deduced; and on the other there is a "developmental" attitude which, in the same situation, investigates the physiological mechanisms underlying the phenomena, in the hope that they will reveal some reason why a conventional genetical situation should produce a peculiar result in this particular case. The consensus of opinion among geneticists confronted with this dualism in flat and uncompromising terms, and with Goldschmidt's unconcealed adherence to the second alternative, was that he had over-stated a good case. Moreover, he tended to call on unanalysed "developmental mechanisms" as a *deus ex machina* to get him out of difficulties in quite as carefree a manner as the statisticians invoke an assemblage of new genes.

Nevertheless there is no doubt that the cleavage of opinion which he indicated is a very real one. Several later speakers felt impelled to announce themselves as belonging to one party or the other—usually this was to the statistical side, which, it was sometimes implied, is the only "real" genetics, developmental considerations falling outside the scope of the pure doctrine and belonging to some other science such as embryology. And the same exclusive attitude has emerged recently in quarters nearer home. For instance, in his Bateson Memorial Lecture Fisher remarked: "There are zoologists, too, who sometimes use the language of genetics. Some of these, however, think that it is a part of the physiology of reproduction; others that it is an aspect of experimental embryology. On these terms what they know of the subject can be accommodated to their outlook and students anxious to learn something of genetics can be diverted to other interests. We need not believe that such misrepresentation is consciously fraudulent. It is sufficiently explained by ignorance of what genetics is about, and ignorance of the means that must be taken to become acquainted with the subject."

Now this alleged conflict between a "statistical" and a "developmental" point of view has always been central to all considerations of the directions in which genetical work should be encouraged in relation to animal breeding and of what form an organization for that purpose should take. The economically valuable qualities of livestock fall in the category geneticists refer to as "quantitative characters"; they indubitably have to be handled by statistical methods; and workers in the theory of statistical genetics have been much concerned with them. In fact many people (including nearly all students who come enquiring about courses in genetics) have been persuaded that applied genetics is mainly a statistical subject. And yet it is obvious that such characters as milk yield, rate of growth, etc., are primarily physiological phenomena. They certainly require investigation from the point of view of statistical genetics, in which the mathematics is part of the essence of the theory; but they also require study in relation to their physiology and development, and if statistical methods are used in this connection, as they well may be, they will be mere tools no more essentially relevant than they are in any other branch of biology. But, except by comparatively few workers, mostly rather outside the main scientific fashion, such as Hammond in this country and Brody in the U.S.A., the relevance of developmental considerations to practical animal breeding has been little recognized.

It has always been my contention, and I made the point again at the International Congress with reference to Goldschmidt's address, that what one should strive for is not a picking of sides between "statistics" and "development", but a union of the two. They usually deal with rather different types of problems, both of which, however, are of great importance. Even within the field which is normally considered that of quantitative genetics, the conflict between them is based on a misunderstanding. All genetical theories of quantitative inheritance always do and always must involve certain suppositions about the ways in which genes interact during development; but some types of such interaction, such as dominance, epistasis, etc., are accepted so much as commonplaces among geneticists that it is often forgotten that they are essentially "developmental genetical" or embryological ideas. There is no reason why these notions should be classed as "genetics" and perfectly proper concepts to introduce into biometrical theory, while newer ideas on which research is still proceeding should be regarded as interlopers against which the purity of genetical doctrine has to be safeguarded. It is not either the statistician or the developmentalist who is wrong, but rather those who think it is necessary to be exclusively either one or the other.

The Theory of Quantitative Genetics and Animal Breeding

The basic idea that "quantitative characters" such as milk yield, weight, etc., are controlled by many genes each of small effect was laid in the practical experimentation of a number of workers, mainly American, between 1910 and 1920. Towards the end of this period, biometrical theories of the phenomena began to be worked out by Weinberg, Fisher, Wright and Haldane. It is important to realize that these theories were originally based on drastic simplifying assumptions. The genes are supposed, in the basic theory, to react with one another in simple ways, each locus adding a certain quota to the genetic constitution irrespective of what genes may be present at other loci; further, the effects of the environment are separated off from the rest by the mathematical treatment and put aside into a category where they can be forgotten; and the need to understand the developmental system underlying the character is circumvented by choosing that scale of measurement which best conceals its peculiarities.

For some years immediately after the development of these theories, rather little experimental work was carried out directly in connection with them, and the subject advanced mainly in the two derived fields of the evolution of populations (mainly by Dobzhansky and Wright) and animal breeding (mainly by Lush, a pupil of Wright). As might be expected, it was found that although the existing biometrical theory worked in a rough and ready way, it was far too simple to account for everything. Attempts were made to improve it by still more ingenious ways of compensating for non-additive gene interactions, environmental effects and particularities of development; but the alternative approach, of trying to understand these phenomena in their own right, with a view to incorporating them explicitly into the theory, was almost neglected. These tinkerings with the basic theory have, however, not been very successful. For instance, even such a confirmed statistician as Sewall Wright has claimed that in some of the more complex analyses information which was immediately visible in the crude data actually became lost in the mathematical apparatus and is no longer present in the final answers.

Among the leading quantitative geneticists assembled at the research conference at Pavia, there was a rather general feeling that some new outlook is needed. This was most strongly expressed by Lerner, whose book on Population Genetics and Animal Improvement, written while he was in the Institute at Edinburgh as a guest of the Poultry Research Centre, is the most recent major summing up of the field. The main challenge to this view came from Fisher who maintained that the theory he had originally expounded was still quite adequate, but this claim was somewhat prejudiced by the well known opposition of Fisher to the major change which has taken place in this field since the original theory was put forward, namely the developments associated with the name of Sewall Wright. This opposition has given rise to a rather bitter controversy within the field of statistical genetics, not only as to the value of the method of path coefficients employed by Wright but also concerning the content of the theories to which this method has led him. The importance of the problems raised by the practical studies of such colleagues of Wright as Dobzhansky on the evolutionary side and Lush in the field of animal breeding cannot, however, be overlooked. Putting the matter in the most general way, those problems arise from the fact that quantitative characters often do not behave in inheritance as though they are controlled by independent additive genes, but rather as though they are "integrated" or "co-ordinated" in some way. One attempt to cope with the situation has been made by Mather in terms which are "statistical" in Goldschmidt's sense. That is to say, he postulated some purely genetical complications to explain the appearance of integration, suggesting that there is a special category of genes concerned with such characters, and that they are linked together into balanced complexes. This theory has, however, not been regarded as adequate in general, although it may apply in particular cases.

Another attempt to advance beyond the old theory was discussed by Lerner at the Inter-

national Congress. He had realized that the problem is not solely genetical, but that the integration is largely a property of the developmental system producing the character. He therefore laid great stress on the concept of developmental "homeostasis," (or "canalisation"). This means, in simple terms, that an organ or physiological system has a certain norm which it tends to attain and which it is difficult to persuade it to depart from. I believe the idea is, potentially, important for an understanding of the genetics of complex physiological entities such as growth rate or milk yield; but Lerner seemed to me unduly optimistic in thinking that he had found a complete explanation of it in one single mechanism. He suggested that the homeostasis (or canalisation) is always due to the animal being heterozygous, i.e. containing two slightly different alleles for every gene, so that one allele can reinforce or counterbalance the other. But this cannot be generally true, since canalisation can occur in respect of genes of which the organism contains only one.

—C. H. WADDINGTON. Excerpts from the Annual Report of the Institute of Animal Genetics, Edinburgh University. 1952-1953.

SECOND TWIN APPEAL FOR MULTIPLE SCLEROSIS STUDY

THERE are 300 to 400 sets of identical twins in the United States where one or both members of the pair is afflicted with multiple sclerosis, is the conclusion reached through recent studies by Dr. Leonard T. Kurland, Chairman of the Committee on Epidemiology of the National Multiple Sclerosis Society, 270 Park Avenue, New York City.

Dr. Kurland's figure was arrived at following the location of 33 sets of twins, one of each pair being a multiple sclerotic, in response to a nation-wide appeal made by the National Multiple Sclerosis Society. This search was initiated in an effort to aid scientists at the University of Illinois under the direction of Dr. Roland P. Mackay in their investigation of the possible causes of multiple sclerosis, a disease whose cause and cure are not yet known.

To further its "Twins Study" begun last fall, the National Multiple Sclerosis Society is issuing another appeal to locate the approximate 350 "missing" sets of twins, according to an announcement made today by Dr. Harold R. Wainerdi, Medical Director of the Society.

"Nature presents us with a ready-made laboratory experiment in the situation of identical twins in determining the relative importance of possible environmental and genetic factors," said Dr. Wainerdi. "Through our second appeal, we hope as well to hear from non-identical or fraternal twins who will serve as a control in the investigation of the role which heredity may play in multiple sclerosis."

The National Multiple Sclerosis Society in cooperation with its sister organization, the Multiple Sclerosis Society of Canada, is also seeking to locate identical and fraternal twins who have this disease in Canada. Since the population of Canada is 9% of that in the United States, it is expected that there would be about 40 identical twinships in Canada meeting the requirements of this study.

Persons who are members of identical or fraternal twinships, one or more of whom is suffering from multiple sclerosis, or who may know of twins either identical or fraternal who have this disease, are urged to communicate with Ntinos Myrianthopoulos, geneticist-in-charge of Multiple Sclerosis Studies, the Dight Institute for Human Genetics, University of Minnesota, Minneapolis, Minn.

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